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An Ecological Analysis of the Plant Communities of Piedmont, North Carolina

Henry J. Oosting*

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Introduction

A detailed knowledge of successional trends and the ecological structure of natural plant communities contributes materially to successful silvicultural practice and forest management. The establishment of the Duke Forest in 1931 as well as the general expansion of forestry interest in the south made it desirable, for practical reasons, that such ecological information be available for the Piedmont Plateau Region of North Carolina. A purely scientific interest in an area heretofore not intensively investigated suggested the need

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for a community analysis which would serve as a foundation for further ecological work. Furthermore, changes in natural vegetation will be increasingly pronounced as the forestry program progresses, and as a matter of historical record, there should be available a characterization of the original vegetation in as complete a form as possible.

Objectives of such a study, as originally conceived, were:

1. To determine, for this area, the natural groupings of plants with respect to their habitats and the changes in these communities with respect to time.

2. To learn, if possible, why these communities occur as they do.

3. To determine possible plant indicators which are satisfactory criteria of the character of the various habitats.

The reasons for undertaking this investigation have strongly influenced the style of presentation. The primary objective was to put on record the general ecological and botanical characteristics of the natural plant communities of the region. It was presumed that such information would be used to the greatest extent by local investigators and students, and secondarily by those elsewhere. This is not intended to imply that this report is only of local significance. The generalizations at least, apply to a large part of the lower Piedmont Plateau, probably from Alabama to Virginia. Specific details are particularly applicable to most of the Piedmont area of North Carolina. Inquiries over a period of years have indicated interests ranging from the technical problems of botanists, foresters and zoologists to practical questions by farmers and home owners. It appeared therefore, that the majority of readers would be best served by (1) keeping terminology at a minimum consistent with clarity and (2) by presenting the information as simply as possible without detracting from its ecological sgnificance. To this latter end graphic methods have been used to show broad relationships. No new concepts or radical interpretations are introduced although application of the phytosociological method to a regional successional study has not been done before in the United States.

The Region and its History

The Piedmont Plateau is an ancient peneplain, which, being long subjected to erosion by numerous streams, has today a rolling topography. Drainage is excellent, for intermittent or permanent streams occupy almost every depression. There are no extensive upland areas which are not dissected by drainage lines, large or small. On the west where the Blue Ridge mountains rise rather abruptly the plateau has an altitude of about 1000 feet. Eastward the surface slopes gently for some 125 miles in North Carolina to 400 or 500 feet at the Fall Line which marks the transition to the lower, level Coastal Plain (see Bowman, 1911).

The soils are residual except in the bottomlands, where new alluvium is deposited almost every year. The most extensive uniform areas of soil are

largely derived from sedimentary rocks. These are mostly sandy loams with clay subsoils. Igneous intrusions, large and small, have weathered to form fine-textured soils of a number of distinct soil series which, because of their mode of origin, abruptly interrupt the soils of sedimentary derivation. The result is a mosaic of soil types, none of which is continuous over large areas. Each has its physical and chemical characteristics and, not infrequently, the best and poorest soils may lie side by side. The mineral soil is exclusively acid in reaction, ranging from pH 5.5 to pH 7.0 (Coile, 1933).

The mildness of the climate is indicated in the records for Durham and Chapel Hill. Zero temperatures are rare and of short duration. The growing season is long, 200 days or more. Temperatures of 100° F. occur in any month from June through September. Annual precipitation is adequate, averaging 47.15 inches for Chapel Hill over a 57 year period. In general it is evenly distributed throughout the year with a somewhat higher amount in summer than in other seasons. Snowfalls are infrequent and practically of no consequence.

In the early days of settlement, large tracts of forest were cleared for cultivation. Land was cheap and little thought was given to agricultural practices that would maintain soil productivity. The heavy winter rains soon washed away the best of the topsoil from unterraced fields and, after several years of cultivation without fertilizing, they became relatively unproductive. It became common practice to abandon such fields and clear new land. This procedure has continued to the present day, although lands now being cleared have usually been cultivated before, in some instances probably more than once. Piedmont farm land is therefore an irregular patchwork of fields and forested areas of all sizes, the latter usually having grown up on previously cultivated land. Since many farmers clear some land every year and abandon a proportionate acreage, a small farm may have timber stands of several ages represented. Individual stands are usually even-aged.

Such was the picture of most of the Piedmont region of North Carolina in 1931 and the 5000 acre Duke Forest area, established in that year, was a fair sample of the whole. Included in the area were home sites, cultivated fields, fields lying fallow and fields which had been abandoned for periods varying from 10 to 100 years. In addition there were stream margins and bottomlands too wet or too narrow to have been cultivated at any time and bluffs and rocky ridges or knolls which, apparently, had never been cleared. With representative areas so conveniently at hand it was only natural that most of the detailed studies should be made upon the Duke Forest or in its vicinity.

Methods

Requisite to such a study is a broad working knowledge of the flora. For many years Dr. H. L. Blomquist has botanized in this vicinity and by his thorough familiarity with species and habitats he was able to give invaluable assistance in the initiation of this work. In addition he cheerfully contributed

assistance with taxonomic problems whenever called upon. The contributions made by others to the progress and completion of this study have been invaluable. All members of the Botany Department staff have given freely of their time and thought when called upon, as have several members of the staff of the Duke School of Forestry. Their assistance is acknowledged with sincere thanks. A special word of appreciation is due to Drs. L. E. Anderson, T. S. Coile, E. S. Harrar and P. J. Kramer for critical reading of the manuscript and to my wife for her many hours of assistance in the field.

Preliminary ecological work was begun in 1933 and observations have continued to the present. Although more intensive work was possible some years than others, observations are included which were made during seven growing seasons. The first summer was devoted to a preliminary survey and reconnaisance. Tree and reproduction counts were made in forest stands and species lists were compiled for the various types of habitats. Collections were made as complete as possible, so that, almost without exception, the species mentioned in this report are all represented by specimens in the Duke Herbarium.

Following these preliminary observations the investigation proceeded largely along phytosociological lines. This is particularly true of the studies of communities representing phases of the major trends of succession.

Only those communities were used for study which were evenly stocked and in which there was little or no evidence of disturbance of any kind. Unless the same general conditions were found repeated in several localities, it was assumed that a single instance might be an exception. Again, only those stands were used for sampling which were uniform throughout as well as extensive enough to permit well distributed quadrats and still leave a reasonable transition area around their margins.

Following the preliminary counts, all detailed work was done on a quadrat basis. Because of the limited extent of many of the stands, it was decided to use ten quadrats per stand for each stratum sampled. Sizes of quadrats were originally determined by the use of species-area curves as discussed by Cain (1934). The general procedure was much as described by Billings (1938). Three sizes of quadrats seemed necessary for complete sampling of forest stands. They were, a tree size, shrub-trangressive size, and herb size. The introductory studies in mature forest stands indicated that, when done in series of ten, the minimum areas for these quadrats should be not less than 10 x 10 m., 4 x 4 m., and 2 x 2 m. respectively. In young pine stands especially, these sizes are probably somewhat larger than necessary, but the extra labor was not excessive and all data are thus on a comparable basis.

Recently, Cain (1938) has shown that the conclusions drawn from a species-area curve may be profoundly influenced by the mere mechanics of its construction. The ratio of the length of x and y axes will determine the point of greatest deflection in the curve. However, when deciding upon the size of these quadrats, the break in the curve was interpreted liberally and,

having used sizes well above the minimum indicated, it seems reasonable that the data obtained represent adequate sampling.

In all sampling procedure the quadrats were distributed along lines, usually two, which traversed the stand paralleling its longest axis. The quadrats were evenly spaced along these lines and always as widely as possible. Each successively smaller quadrat was placed within the larger so that, along the lines, ten sets of plots of three each were regularly spaced. The smaller quadrats always occupied the same relative position within the larger.

In the quadrats used for tree sizes (10 x 10 m.) two strata were distinguished. The overstory individuals were recorded separately from the understory. The latter included all individuals over ten feet tall or an inch or more in diameter. In the 4 x 4 m. plots all other woody individuals were tabulated but regularly separated into groups including those over one foot tall or less than one foot tall.

There were distinguished then, four woody strata or size classes, a dominant layer, a subdominant layer, a stratum of tall shrubs and transgressives, and finally one of seedlings or low shrubs. Herbs were recorded as found, regardless of size.

The Major Habitats and Communities

Virgin forest, as it was before the local appearance of the white man, is today completely lacking in the region. Only small isolated stands of relatively great age (200-300 years) and relatively little disturbance remain as apparent relicts of what the original extensive forest of the uplands must have been like. Such stands are few since little of the area has been free from disturbance by man at some time. The practice of cultivation and abandonment has been used on almost every tillable piece of soil regardless of extent. Cultivation of a quarter acre field or even less is not uncommon. Exceptions to such treatments are usually associated with ridges and knolls unfavorable for cultivation or with inaccessible situations such as high or steep bluffs. Stands on such areas and the hardwoods on better sites which are usually selectively cut are the remnants of the original forest.

Since, as will be shown, fields are almost invariably occupied by pine which forms closed stands within 10-15 years, the greater part of the territory is dominated by pine. Thus pure stands or pine dominance indicate cultivation at some previous period. In spite of the abundance of pine few stands can be found which are older than 60 years and are suitable for phytosociological study. Usually before this age the trees can be used for lumber and, especially on good sites, thinning or clear-cutting for cordwood is possible at a much earlier age. There are then, many stands available for study representing the younger age classes, a much smaller number of middle-aged stands and very few mature or over-mature stands.

Bottomlands and flood plains as well as the more extensive uplands may support pine forest after cultivation. These moister sites, however, especially if

subject to spring flooding, are more characteristically occupied by hardwoods. Floodplain soils are alluvial, but texture and drainage are frequently variable because of the width of the flood plain, the depth to which the stream has cut, and the existence of depressions and seepage areas. The occurrence of lowland species and the development of communities is strongly affected by these moisture factors which are related to the physiographic maturity of the site. In general, lowland drainage is too perfect to permit extensive undrained depressions and consequently truly marshy grounds are rare in the section. Some cleared flood plains are too wet for cultivation and these are often mowed for hay so that succession is held in check and a moist meadow condition is maintained for years.

Early stages of primary succession in lowlands may be observed on islands forming in streams. Occasionally mature islands may be found which are too small or inaccessible to cultivate and the vegetation they support indicates the trend of primary bottomland succession.

Surface erosion has been, and still is, fairly general on cultivated fields in the Piedmont. Since it has been the rule rather than the exception, erosion may be disregarded in a general consideration of secondary succession except where it has been so severe as to remove all of the upper soil strata. When this has occurred there are local extremes of gulleying where only the B and C soil horizons are available for occupancy by plants. Establishment and development of vegetation on these raw subsoils is classed here as primary succession.

Bare rock provides another habitat characterized by primary succession. Flat or domed exposures of granitic rock, sometimes acres in extent, are frequent along the lower margin of the Piedmont Plateau. Others occur to the west on the occasional outliers of the mountains in the upper Piedmont. Over most of the area between, this succession is restricted to the rocks and boulders which may occur almost anywhere but which are most frequent along bluffs and streams.

Additional habitats of a special nature which have their own peculiar groupings of species are abandoned home-sites and roadsides. The average farm tenant's home and out-houses are not elaborate and when an acreage ceases to be productive the entire place may be abandoned. Roadsides, as elsewhere, have, in addition to the species of forest and fields, a considerable number of species particularly adapted to the conditions of exposure, clearing, cutting, and grazing. Regardless of soil or topography the roadside community is much the same throughout the area.

There is finally, fire, a factor which may modify the entire appearance and trend of development in a short time. Fire is fortunately much less frequent in the Piedmont now than a few years ago, but constant vigilance is necessary to keep it at a minimum. Even the care and watchfulness which Duke Forest receives do not insure complete protection and small fires occur now and then.

Since the majority of the communities present in the area appear on disturbed habitats they are of a secondary nature. Secondary succession is

notably more rapid than primary and, with the rapid growth rates of woody species in this section, one can hardly describe a community except from a dynamic viewpoint. The presentation which follows will attempt to give an adequate picture of the major communities as they occur but the treatment of each will involve placing it in its successional position.

I. Secondary communities will be considered under two major headings:
   A. Abandoned Fields.
   B. Fire.
   C. Cutting.

II. Primary communities, much less frequent, and so localized as to be of relatively little importance economically, will be treated as they are related to:
   A. Floodplains.
   B. Bluffs.
   C. Erosion areas.
   D. Rock outcrops.

I. Secondary Communities

A. Communities of Abandoned Fields

1. upland

Succession following abandonment of upland fields is represented by distinct communities which follow each other rapidly in the early stages. Crafton and Wells (1934) present a general discussion of these early stages with emphasis upon the factors producing minor variations. Their use of the term "prisere" seems unfortunate for, as Clements (1916) originally proposed, "primary successions . . . arise . . . upon surfaces exposed for the first time. Such areas have in consequence never borne vegetation before. Secondary successions arise on denuded soils, . . ." Since the development of vegetation on these abandoned fields is obviously related to cultivation, the bare areas are of a secondary nature and the succession is secondary.

When the Duke Forest was established many fields were immediately put out of cultivation and others were abandoned for planting in the near future. Today these fields support flourishing plantations or natural stands of pine. In the summer of 1933 there were more "turned out" fields on Duke Forest than there ever will be again. These included fields previously abandoned by farmers as well as fields newly abandoned because of the forestry program. Many of the latter were still in a relatively productive condition and relatively little eroded. As a consequence there were available for study, several examples each of fields abandoned from one to five years and of several soil types. Here then, was a good variety of conditions within a restricted area and all were available for study.

All relatively uneroded fields which had been abandoned for one, two or three years were located and studied. Some of these fields were small and it

Fig. 1. *Leptilon canadense* dominance on upland field abandoned for one year (photographed in July). Fig. 2. Autumnal aspect of field abandoned for two years. *Aster ericoides* dominant. Fig. 3. Upland field abandoned for five years. *Andropogon virginicus* dominant, scattered composites mostly species of Eupatorium and Solidago. Young pine *(P. taeda)* well established.

was thought that ten quadrats one meter square would give an adequate sample. Subsequent consideration of the results indicated that, with data from several fields for each age class, a single series of ten quadrats for each field was adequate.

a. *Digitaria-Leptilon* (one-year fields)

Five fields were studied which had been abandoned for one year (Fig. 1). A summary of the counts for individual fields and for the five collectively is given in Table 1. The most conspicuous species on these fields are crabgrass *(Digitaria sanguinalis)*[1] and horse weed *(Leptilon canadense)*. The counts show that crabgrass makes up 63% of all individuals present and that it is uniformly distributed, for, based upon 50 quadrats in 5 fields, its frequency is 100%. Horse weed, with only 11% of all individuals, is likewise a dominant and characteristic species. Larger than crabgrass it is more conspicuous and at the same time has an average frequency of 94%, on three fields 100%.

TABLE 1.—Density* and frequency** of species appearing in five fields abandoned for one year.

Fields		I	II	III	IV	V	Summation values
Allium vineale	D	1.1	1.4	0.2		3.5	124
	F	40	50	10		70	34
Ambrosia artemisiifolia	D	3.8		1.3	0.1	4.7	198
	F	30		60	10	80	36
Antennaria plantaginifolia;	D		0.4		2.7	0.3	68
A. fallax; A. parlinii	F		20		90	10	24
Asclepias incarnata var. *pulchra*				0.1			2
				10			2
Cassia chamaecrista					0.1		2
					10		2
Cyperus compressus		12.0	14.3	0.1			528
		40	50	10			20
Digitaria sanguinalis		60.6	84.0	14.5	137.5	110.0	8132
		100	100	100	100	100	100
Diodia teres		1.8	0.1	0.1	3.4		108
		40	10	10	50		22
Eragrostis pilosa		1.6	0.1	1.3	0.2		64
		10	10	60	10		36
Euphorbia nutans						1.2	24
						50	10
Fimbristylis autumnalis		0.8					16
		10					2
Gnaphalium obtusifolium				0.1	0.7		16
				10	40		10

1 Authorities for all specific names, and the common names used are listed in the appendix.

* The average number of individuals of a species per quadrat in a stand. This is no indication of how these individuals are distributed in the stand.

** The number of quadrats in which the species occurred as expressed in percent of total quadrats used. This value is thus an expression of the uniformity of distribution of a species in a stand.

TABLE 1.—(Continued)

Fields	I	II	III	IV	V	Summation values
Gnaphalium purpureum	0.9	3.6	1.3	3.6	1.9	226
	20	90	50	80	50	58
Helenium tenuifolium		0.1				2
		10				2
Hypericum drummondii	0.2					4
	10					2
Hypericum gentianoides	0.5	0.1	0.5	27.6	6.4	702
	30	10	40	100	100	56
Ipomoea lacunosa					0.2	4
					10	2
Ipomoea pandurata			0.1			2
			10			2
Juncus tenuis	8.6		0.1	0.1	0.2	180
	70		10	10	10	20
Leptilon canadense	2.0	34.4	5.2	26.5	5.3	1468
	90	100	100	100	80	94
Lespedeza striata		0.1		0.1	0.5	14
		10		10	20	8
Panicum dichotomum			0.1		1.3	28
			10		20	6
Passiflora incarnata		0.1				2
		10				2
Plantago aristata	0.7		1.5	0.1	1.8	82
	20		60	10	50	28
Polypremum procumbens	4.2					84
	20					4
Polygonum pennsylvanicum	1.0		0.2			24
	40		20			12
Rumex acetosella		0.7		11.1		236
		10		50		12
Scutellaria integrifolia					0.1	2
					10	2
Solanum carolinense			0.1		0.5	12
			10		20	6
Solidago (rosette)			4.1			82
			80			16
Stenophyllus capillaris	14.0	0.1	0.8	0.1	0.6	312
	80	10	60	10	40	58
Tecoma radicans	0.2		0.2			8
	20		20			8
Xanthium canadense	2.2				1.0	64
	10				10	2
Totals	126.2	140.3	31.9	213.9	139.5	
	18 spp.	17 spp.	20 spp.	18 spp.	20 spp.	35 spp.

Species with the next highest distribution values are *Cyperus compressus* and *Hypericum gentianoides*. The former, small and localized, has its highest frequency in a single field and is not recorded at all for two fields. Pineweed, however, has a general distribution and, in spite of its low density, is a rather typical species. It is probably more conspicuous during the winter months than at other times for its tough, wiry branches remain erect well into the next season.

These counts were made in late summer and fall. More recent observations indicate that certain annuals like *Gnaphalium purpureum* and *Lespedeza striata* are far more abundant in spring and early summer than the data indicate.

Regardless of the treatment, condition or soil type, it is apparent that a field abandoned one year is characterized by Digitaria-Leptilon dominance. Numerous annuals of the "weed" type are associated in varying numbers. The concentration of crabgrass is probably determined to a certain extent by the cultivation of the previous season. If the average cultivated field is not kept clean the predominant weed at the end of the season is crabgrass. Often it forms solid mats. Such fields undoubtedly produce a greater number of plants of crabgrass during their first year of abandonment than would have been produced in clean fields. A number of the species predominating in old fields may have large numbers of viable seeds buried in the soil, especially in earlier stages of succession (Oosting and Humphreys, 1940). Some seeds remain viable in the soil for long periods and these species may appear at unexpected times in later stages of succession when the soil is disturbed. Other species may appear only in a single stage of old field development, although their seeds are present and remain viable for several years longer.

Indicators of erosion, included in this series, are *Plantago aristata* and *Diodia teres*.

The complete absence of *Linaria canadensis* and *Rumex hastatulus* from these lists is of interest for, only slightly eastward in the coastal plain, and in the sand hill region to the south, they assume aspect dominance in early summer. They seem to be most common, however, on deep sands and appear only occasionally in the clayey soils of the Piedmont.

b. *Aster-Ambrosia* (Two-year fields)

Seven fields, which had been abandoned for two years, were studied intensively (Table 2). Again, as in the one-year fields, crabgrass is indicated as the most abundant and most uniformly distributed of all species present. By count horse weed too is still important. In spite of their numbers however, neither is a dominant, for on two-year fields they are both overtopped by *Aster ericoides* (Fig. 2) and *Ambrosia artemisiifolia*. These two species are bushy and ordinarily two to four feet tall. Together or individually, they are the character species of two-year fields because of size, numbers, and conspicuousness. Aster is more constantly present and more uniformly distributed. Ragweed predominates only on the poorest fields. Many of the species of the open one-year fields are excluded the next year by shade and competition. Others, like horse weed, maintain their numbers, but are so reduced in size as to be of no real importance. *Leptilon canadense* may often be four to six feet tall on one-year fields. Here, in competition with the massed plants of Aster and Ambrosia, it is usually no more than six inches. *Hypericum gentianoides* is similarly dwarfed but relatively less than other species.

Again the relatively high numbers of *Aristida dichotoma* and *Plantago*

TABLE 2.—Densities and frequencies of species found in seven fields abandoned for two years.

Fields	VI	VII	VIII	IX	X	XI	XII	Summation values
Allium vineale	D 3.6				2.6	1.2	1.6	129
	F40				70	40	60	30
Ambrosia artemisiifolia	D10.5	0.7	1.2	7.2	3.6	1.7		356
	F100	40	50	90	90	50		60
Andropogon spp.		9.9	1.5	14.1	0.8	1.7	4.0	458
		100	80	100	60	50	70	66
Antennaria spp.			0.2				35.3	508
			10				90	10
Aristida dichotoma	1.0			74.3			10.0	1218
	10			60			10	11.4
Asclepias incarnata var. *pulchra*					0.1			2
					10			1.4
Aster ericoides	0.7	9.3	1.9	4.0	15.3	19.7	4.1	787
	20	100	80	70	100	90	80	77.1
Cynodon dactylon				0.7				20
				10				1.4
Cassia chamaecrista	0.6	0.2	0.6				0.3	25
	20	10	30				10	10
Croton glandulosa				0.7				10
				30				4.3
Cyperus aristatus						0.8		12
						10		1.4
C. compressus	0.8	0.5		0.1				20
	30	20		10				8.5
C. retrofractus	0.4							6
	20							2.8
C. retrorsus					0.1			2
					10			1.4
Daucus carota	1.2	0.1	0.1	8.0		0.9		147
	10	10	10	100		10		24.2
Digitaria sanguinalis	10.8	15.2	26.8	27.1	17.5	4.3	78.0	1570
	90	70	100	100	80	60	90	84.3
Diodia teres	7.6	1.1	8.5	3.1	0.4		10.8	450
	40	30	70	60	20		50	38.6
Eleusine indica	1.3							1.9
	20							2.8
Eragrostis pilosa	0.1							2
	10							1.4
E. pectinacea		0.2						3
		10						1.4
E. refracta			0.1	1.1	0.1		1.5	40
			10	30	10		30	11.4
Eupatorium capillifolium						0.2		3
						10		1.4
E. hyssopifolium				0.2			0.2	6
				10			10	2.8
Euphorbia nutans		0.3		5.4	0.9	2.2		126
		20		90	70	60		34.3
Gnaphalium obtusifolium		0.1		0.2		0.2	0.8	19
		10		20		10	20	8.5
G. purpureum			1.4			10.0	6.1	250
			20			50	60	18.6

TABLE 2.—(Continued)

Fields	VI	VII	VIII	IX	X	XI	XII	Summation values
Cymnopogon brevifolius		0.6	0.4	1.4				35
		20	10	10				5.7
Helenium tenuifolium	0.1						1.8	2.7
	10						10	2.8
Hypericum drummondii	1.0			0.4		0.4		26
	30			10		10		7.1
H. gentianoides	11.9	3.3	40.8	0.9			40.0	1386
	100	50	100	30			90	52.9
H. punctatum						0.5		7
						10		1.4
Ipomoea hederacea			0.1					2
			10					1.4
Ipomoea lacunosa			0.5	0.1	1.5			30
			30	10	70			15.7
I. pandurata			0.1					2
			10					1.4
Juncus tenuis	4.4	0.1	0.4			1.0	0.6	93
	70	10	20			10	40	21.4
Lactuca canadensis						0.9		13
						40		5.7
Leptilon canadense	1.7	2.2	33.3	0.2	0.4	26.4	13.5	1111
	30	50	100	10	20	90	100	57.1
Lespedeza striata	0.7	0.2	0.2		1.1	0.1	0.4	32.9
	30	10	10		20	10	10	12.9
Oxalis stricta		0.2	0.3	0.2	1.0	0.6		33
		10	10	20	10	30		11.4
Panicum capillare					0.2			3
					10			1.4
P. dichotomum				1.6	5.4			100
				40	70			15.7
Passiflora incarnata	0.2	0.5						10
	20	30						7.1
Plantago aristata	9.8	17.0	8.6	12.9				691
	60	60	40	30				27.1
P. lanceolata	1.9			0.9				40
	30			10				5.7
Polypremum procumbens							1.3	19
							40	5.7
Potentilla canadensis				7.5				107
				40				5.7
Pyrrhopappus carolinianus						0.1		2
						10		1.4
Rumex acetosella	7.6	2.9		0.4				156
	50	20		10				11.4
Scleria pauciflora						0.2		3
						10		1.4
Scutellaria integrifolia					0.3			4
					10			1.4
Setaria lutescens				2.8	0.3			45
				20	10			4.3
Sida spinosa	0.2			0.3	0.3			11
	10			10	10			4.3
Solanum carolinense		0.6	0.5	0.2	1.3	0.8	0.5	56
		30	20	20	70	30	30	28.6

TABLE 2.—(Continued)

Fields	VI	VII	VIII	IX	X	XI	XII	Summation values
Solidago caroliniana				3.0				43
				30				4.3
S. juncea				0.2	0.4			9
				20	10			4.3
S. nemoralis		0.1	0.2	1.2		0.4	0.1	19
		10	20	40		20	10	14.3
Solidago spp. (rosettes)					99.1	21.4	1.8	1749
					80	30	20	18.6
Sporobolus poiretii				4.5				64
				10				1.4
Strophostyles umbellata			4.2	0.3				64
			100	10				15.7
Tecoma radicans			0.2		1.2	0.5	2.2	59
			10		80	30	90	30
Xanthium canadense and	0.6			1.3	0.7	1.0	0.1	53
X. echinatum	40			40	30	20	10	20
Totals	776	650	1325	1865	1552	978	2150	
	24 spp.	21 spp.	23 spp.	33 spp.	23 spp.	24 spp.	22 spp.	61 spp.

aristata indicate that there were erosion areas within the fields. However, these species are small and their closely concentrated growth habit is shown by their low frequency indices. *Diodia teres,* too is usually found on eroded soil but is not restricted to it.

The high counts for species of Andropogon and Solidago are not in proportion to their importance in these fields. Rather, these counts indicate their importance in years to come. Neither is of any size here. The Andropogon plants, having just started from seed, are rarely represented by more than a small cluster of a few basal leaves and the goldenrods, also very young, have developed only a basal rosette. Species were recorded separately for the latter but identifications were often so uncertain as to make their value doubtful.

c. *Andropogon* (Three-year fields)

Fields undisturbed for three years or more after abandonment are not common. It is general practice to burn off such areas in spring to give improved pasturage or for other reasons. Burned or pastured fields were not sampled and, when it was impossible to determine the history of an area, it was not studied in detail for it seemed best to restrict investigations to those which were known.

Three three-year fields were studied (Table 3). Here Andropogon attains a frequency of 100% and its numbers are increased materially. In addition, almost every individual has formed a clump, often occupying ten times the space of the individuals on two-year fields. The species of Andropogon are not always determinable in summer condition and consequently all were lumped in the counts. *A. virginicus* is the usual species on old fields (Fig. 3) but, locally and always in smaller numbers, *A. ternarius* and *A. elliottii* may also occur.

TABLE 3.—Density and frequency of species found in fields abandoned for three years.

Fields	XIII	XIV	XV	Summation values
Allium vineale	D 0.6		2.7	109
	F20		20	13.3
Ambrosia artemisiifolia	D 0.7		0.1	27
	F20		10	10.0
Andropogon spp.	11.0	11.2	2.0	799
	100	100	100	100
Antennaria spp.		3.5	0.4	129
		60	30	30
Aristida dichotoma		1.4		46
		20		6.7
Aster ericoides	5.1	0.9	0.9	228
	90	50	40	60
Cyperus compressus	0.1		8.7	281
	10		60	23.3
Daucus carota	0.4	0.9		43
	20	20		13.3
Digitaria sanguinalis	2.9	5.7	32.1	1343
	80	80	100	86.7
Diodia teres	1.3	1.0	0.8	43
	20	50	20	13.3
Eragrostis pectinacea		1.1		37
		50		16.7
E. refracta		0.1		4
		10		3.3
Eupatorium capillifolium	2.9	1.6		149
	80	30		36.7
E. hyssopifolium		0.2		7
		10		3.3
Gnaphalium obtusifolium	0.1	0.8	0.5	46
	10	60	30	33.3
G. purpureum	7.0	4.5	0.3	390
	80	70	20	56.7
Helenium tenuifolium		0.4	0.8	40
		20	10	10.0
Hypericum gentianoides	4.1	1.9	29.7	1178
	50	50	80	60.0
Ipomoea pandurata			0.1	4
			10	3.3
Juncus tenuis	2.9	2.1		165
	60	50		36.6
Leptilon canadense	6.4	17.1	45.5	2277
	70	90	100	86.7
Lespedezia striata	0.9	0.8	0.2	63
	20	30	10	20.0
Oxalis stricta		0.1		4
		10		3.3
Panicum dichotomum	0.3	0.2		17
	10	20		10
Passiflora incarnata			0.1	4
			10	3.3
Plantago aristata	3.5	6.6		334
	30	80		36.7
Polypremum procumbens	1.7	1.2		96
	40	40		26.7

TABLE 3.—(Continued)

Fields	XIII	XIV	XV	Summation values
Potentilla canadensis		0.9		30
		20		6.7
Pyrrhopappus carolinianus		0.2		7
		20		6.7
Scutellaria integrifolia			0.2	7
			10	3.3
Solanum carolinense	0.3			10
	10			3.3
Solidago juncea	0.1			4
	10			3.3
S. nemoralis		0.7		23
		20		6.7
Solidago spp. (rosettes)	0.2	0.2	0.2	20
	10	20	10	13.3
Strophostyles umbellata	0.3	0.3	3.3	129
	20	20	100	46.7
Tecoma radicans	1.4	1.1	0.8	109
	100	80	50	76.7
Xanthium canadense		1.8	0.4	73
		20	10	10
Totals	601	684	1298	
	23 spp.	29 spp.	21 spp.	37 spp.

All other species are subordinate to Andropogon. All that have survived grow between the massive clumps of the grass and likewise are overtopped for a good part of the growing season. Considering the competition from the fast spreading Andropogon it is rather remarkable that so many of the annual species of earlier conditions are still present in three-year fields.

SUMMARY—DISCUSSION OF ABANDONED FIELDS

In Figure 4, frequency-density relationships of the species are graphically compared for the three age classes. To a reader unfamiliar with the species and their habits, such a representation might lead to false conclusions. However, the preceding discussion should have clarified what might otherwise appear as discrepancies. The data from all of the meter-square, list-count quadrats are included although each age of field is represented as having been equally sampled.[2] Combining the data for each type of field seems justified, for differences between fields of the same age do not appear to be significant. Relative numbers are indicated for each species by the height of the columns. Frequency, or the uniformity of dispersal in the stands, expressed in percent of quadrats occupied, is shown by the width of the columns.

One-year fields showed thirty-three species. Two of these had disappeared in the two-year fields and thirty-one additional species appeared. The added

[2] The summation values are listed in the final columns of Tables 1, 2, and 3. Densities have been transposed to make them directly comparable to values determined for herbs in the sampling of wooded stands. This tends to slightly overweight the abundance of some of the least common species in old fields and likewise obscures the complete absence of certain species from some fields (presence), but the advantages are obvious.

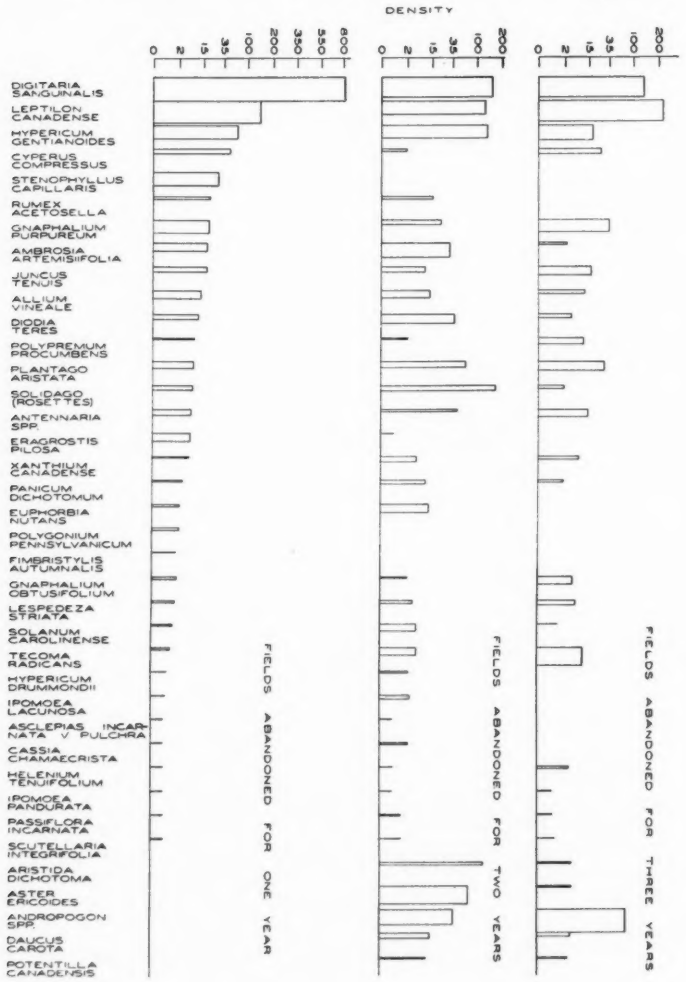
species included *Aster ericoides*, the major dominant of two-year fields, and *Andropogon* spp. which becomes dominant the third year. All other species in this added group are of relatively little importance in a permanent sense, except wild carrot *(Daucus carota)* and dog fennel *(Eupatorium capillifolium)*. During the second year, the Daucus which is constantly present though of low density and frequency, assumes aspect dominance in late June and July. If for any reason Andropogon-dominated fields remain somewhat open, *Daucus carota* maintains itself. The clumps of dog fennel increase in number and size until shaded out by pine. In the open, it is an obnoxious and trying weed. Unless its massive root system is completely dug out, scattered clumps may persist in cultivated fields for many years.

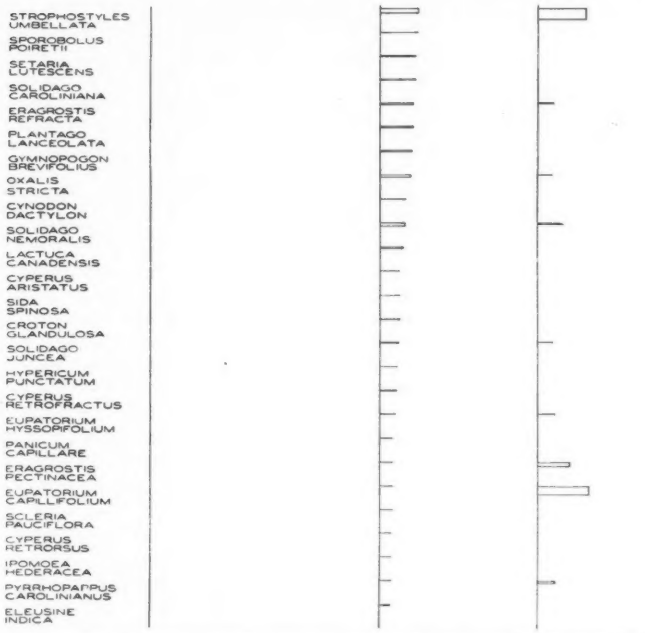
The third year adds only one species to the list while the surprising number of twenty-three have completely disappeared and only thirty-seven species remain. This constitutes a remarkable rise and fall in so short a period. Total numbers of individuals, as calculated for fifty square-meter quadrats per age of field would be 6410 for one-year fields, 6147 for two-year and 4167 for three-year fields. These figures represent a 4% decrease in total number of individuals between the first and second year, followed by a further 32% decrease between the second and third year. The latter tremendous decrease is explainable in terms of the increase in size of Andropogon clumps. Their fibrous root systems occupy most of the soil, and must therefore materially reduce the water and nutrients available to smaller plants. In addition they shade the ground almost completely. Thus by midsummer many of the lesser individuals, unable to compete, have been eliminated.

Repeated observations of many additional fields have shown these generalizations drawn from the data to be essentially correct. From midsummer on, until growth is resumed in the spring, the time of abandonment can be recognized at a glance for the majority of upland fields. *Digitaria sanguinalis* is the characteristic weed of cultivated fields. During the first year of abandonment, crabgrass is codominant with horse weed. The second year, *Aster ericoides* is the conspicuous plant by reason of its size and general distribution but *Ambrosia artemisiifolia* may also be important. By the third year Andropogon assumes dominance and, if undisturbed, maintains itself until the site is occupied by woody stages in succession.

Irregularities in this sequence sometimes occur, but usually only in limited areas. "Bald" spots within otherwise normal fields are usually the result of local surface erosion. Aristida, especially *A. dichotoma*, is the pioneer and may be the important plant for several years. With it, *Diodia teres, Plantago aristata* and several low compact lichens help to build up an erosion resisting mat on the soil surface which eventually permits the establishment of species characteristic of uneroded areas. Ragweed is apt to be more abundant on such areas than Aster. Billings (1935) showed that, on fields from which the top soil had been artificially removed, *Aristida dichotoma, Rumex acetosella, Plantago aristata, Diodia teres, Hypericum gentianoides* and *Ambrosia artemisiifolia* are species which occur more frequently and in greater numbers than on normal

Fig. 4. Changes in density-frequency relationships of species occurring on one, two and three-year fields. The length of the columns represents density, the width indicates frequency. Because of the difficulty of representing absolute values of so wide a range of densities in a single figure they have all been modified by a factor $\frac{(\sqrt[3]{\text{density}})}{5}$.





abandoned fields. Free from the competition of larger species these xerophytic types tend to maintain their dominance for long periods on any area where the subsoil is exposed. Eventually conditions become favorable for the invasion of species typical of uneroded soil.

Burning, cutting and grazing tend to permit more light to reach the soil surface. Under such conditions *Cynodon dactylon* (Bermuda grass) becomes established and, when it does, the rate and trend of succession is modified. Pastured fields are often overgrazed and clumps of composites, including *Helenium tenuifolium, Solidago* spp., *Eupatorium* spp., *Achillea millefolium, Chrysanthemum leucanthemum, Senecio smallii* and *Erigeron ramosus* are typical of such areas. These same species are found in abundance on roadsides which are mowed. They are especially luxuriant when not shaded. Wherever Bermuda grass forms a mat and the composites are well developed the invasion of pine is much delayed. The pine seeds cannot come in contact with mineral soil and germinations are, therefore, infrequent. Such conditions are rare in fields, but most roadsides, homesites, and city lots furnish excellent examples.

d. *Loblolly Pine (Pinus taeda)*

Depending upon the proximity of pine seed supply and also upon seed year, Andropogon dominance may be maintained for a varying number of years. Often within three or four years of abandonment seedling pines may be found between the clumps of broomsedge. Commonly after five years the pines may be seen showing above the grass (Fig. 3). Rarely does a field lie more than five years without some pine making its appearance and commonly ten years will have produced an even aged stand of young pines which, on good sites, will be several feet tall.

Three pines are indigenous to the region *(P. taeda, P. echinata, P. virginiana)*. Duke Forest occupies a peculiar position with respect to their ranges for, although all three appear here, the first is most abundant to the south and east, the second to the west, and the last to the north and northwest. Each tends to appear in pure stands although mixtures, especially of loblolly and shortleaf, are not uncommon. The pure stands and local distribution of the species seem largely determined by the chance of seeding, for all appear to thrive equally well wherever they start. However, observing many stands in a variety of situations leads to a generalization that loblolly occurs most often on the best sites, Virginia pine on the poorest and shortleaf on intermediate ones.

The peculiar position of Duke Forest with respect to the ranges of the three pines is further of interest when it is found that the ranges of other conifers overlap in the general vicinity. Hemlock, characteristic of the mountains, with its best development more than 200 miles to the west, grows naturally in an isolated stand in nearby Wake County. White pine also reaches its eastern limit slightly to the east in a disjunct stand in Lee County. At the same time, longleaf pine, typical of the coastal plain, extends in isolated stands, some distance west of the Forest location. Factors determining the limits of ranges and permitting these remarkable overlaps here, require further study. There are no reasons readily available to explain these apparently anomalous distributions.

Pine growth is rapid in the area. On good sites, a site index of eighty feet in 50 years is not uncommon. With such growth the changes in associated species following establishment of pine, are, as would be expected, abrupt and pronounced. Billings (1938) traced the development of shortleaf pine stands on Duke Forest from youth to maturity. His approach to vegetational analysis as well as treatment was similar to the general plan followed here. At the outset it will suffice to state that the trends and rates of change are similar in both shortleaf and loblolly stands and this makes it unnecessary to review Billings' work in detail. He used only pure stands of shortleaf and consideration will be given here to pure stands of loblolly. Mixed stands do occur but, as an ecological type, these are being disregarded for their characteristics must be intergrading between the closely related loblolly and shortleaf stands.

The data which follow were obtained from upland loblolly pine stands of relatively even age which were well stocked and had not suffered any major disturbance. Lowland stands are similar but differ enough to merit a separate consideration. Six upland stands were studied which ranged in age from 11 to 75 years. Search for usable older stands proved unsuccessful for invariably before this age the timber is merchantable and will have been cut or selective cutting will have ruined the stand ecologically.

An adequate picture of the stands and their relationships can probably be presented best by considering the data from a primarily static point of view and then discussing the interrelationships and successional implications.

Eleven-Year Pine[3]

The stand representative of this age-class had come in on a broomsedge field which was east of a good seed source. Apparently best seeding is received when fields occupy such a position, for winds are prevailingly from the west. Nearest the parent stand the density was greatest while it decreased considerably at the farthest extremity of the field. The counts represent average conditions, for the quadrats were evenly distributed. In the denser portions of the stand much of the old field vegetation had been eliminated but in the more open portions, broomsedge with its associated species was still thriving. Only a few species not typical of old fields appeared in the herb plots.

Only pine was of tree size, other woody species were just becoming established as seedlings or small transgressives. The pines were 8-15 feet tall, a not unusual growth in 11 years on good sites. Because of some irregularity in growth and because all pines appeared to be the same age, no attempt was made to distinguish over- and understory individuals.

The number (density 26.8) and distribution (frequency 100%) of the pines are representative of many young stands. However, there are often much higher densities and then the young trees grow so closely that mortality is great during the early years. Other fields, poorly located for seeding or eroded in spots may develop ragged, irregular young stands. The openings in these stands invariably are seeded within a few years and subsequent growth reduces the differences between individuals. The result is that in later years these differences are scarcely noticeable except that increment borings may show a range of several years of age in the stands which developed irregularly.

Table 4 gives density and frequency values for all the stands of upland pine which were sampled. There are no understory trees when development is comparable to that of the 11-year stand but the reproduction indicates the potential understory to come. Pine seedlings are the most abundant (16.2) and widespread (80%). Evidence from the more mature stands however, indicates

3 Hereafter the wooded sites will be designated by the age of the trees and not by the time since abandonment. Since there may be a variation of as much as five to ten years in the time required before tree dominance this seems the logical procedure.

TABLE 4.—Density and frequency of trees in four size classes, shrubs, vines, and herbs in a successional series of upland loblolly pine stands.

Age of stand	11	22	31	34	42	70–75
Overy story trees						
Pinus taeda	D 26.8	18.2	15.1	12.2	12.5	3.4
	F 100	100	100	100	100	90
P. virginiana	D	0.1				
	F	10				
Fraxinus americana			0.2			
			10			
Liquidambar styraciflua				0.6		
				50		
Quercus rubra				0.2		
				10		
Under story trees						
Pinus taeda		1.3		1.2		
		40		60		
Liquidambar styraciflua		4.5	0.2	8.7	1.5	0.1
		90	20	90	60	10
Nyssa sylvatica		1.5	3.1	0.3	0.4	2.2
		60	30	20	20	50
Oxydendrum arboreum		1.2	1.7	8.1		2.3
		60	50	80		40
Diospyros virginiana		1.1	1.2	1.1	0.9	0.4
		30	60	30	30	10
Carya spp.		0.7	1.3	0.2	0.2	1.2
		40	30	20	20	60
Cornus florida		0.6	2.1	0.8	0.3	3.5
		50	70	50	30	100
Juniperus virginiana		0.5	0.2	0.4	0.1	
		40	20	20	10	
Fraxinus americana		0.2	0.1	0.5		0.5
		20	10	10		50
Cercis canadensis		0.1	0.3	0.1		
		10	20	10		
Juglans nigra			2.4			
			20			
Acer rubrum			1.4	0.3	0.1	0.9
			40	20	10	40
Quercus rubra				0.7		
				50		
Liriodendron tulipifera				0.6		0.2
				40		10
Quercus stellata				0.3		
				20		
Morus rubra				0.1		
				10		
Quercus marilandica					0.2	
					10	
Q. alba					0.1	0.1
					10	10
Prunus serotina						0.6
						40
Transgressives						
Pinus taeda	15.6	2.5	3.1	3.8	5.6	2.5
	80	30	40	40	50	30

TABLE 4.—(Continued)

Age of stand	11	22	31	34	42	70–75
P. virginiana	0.6					
	10					
Cornus florida	8.8	25.6	94.4	14.4	5.6	201.0
	50	50	80	70	30	100
Liquidambar styraciflua	3.1	15.0	1.3	53.8	3.8	1.3
	30	70	20	100	50	10
Acer rubrum	2.5	16.9	67.5	10.6	1.3	5.0
	40	70	100	80	20	20
Quercus velutina	2.5	0.6	4.4	2.5	0.6	2.5
	30	10	50	20	10	40
Nyssa sylvatica	2.5				3.1	6.3
	10				20	30
Juniperus virginiana	1.9	1.9	1.3	1.9	3.8	1.3
	30	20	20	30	40	20
Liriodendron tulipifera	0.6	0.6	0.6	0.6		
	10	10	10	10		
Oxydendrum arboreum	0.6	0.6	18.8	7.5		
	10	10	30	30		
Sassafras officinale		15.0		0.6		0.6
		30		10		10
Quercus rubra		7.5		13.1		
		60		60		
Diospyros virginiana		6.3	13.1	10.0	6.3	3.1
		50	70	60	30	20
Carya spp.		1.9	13.1	4.4	9.4	8.6
		30	90	50	70	80
Ulmus alata		1.9	0.6		1.9	
		10	10		20	
Quercus alba		1.3	7.5		1.9	6.9
		30	60		20	80
Cercis canadensis		0.6	2.5	5.6		
		10	40	60		
Quercus coccinea		0.6	5.6		3.8	1.3
		10	60		60	10
Fraxinus americana		0.6				
		10				
Juglans nigra			3.8			
			20			
Quercus borealis var. *maxima*			0.6	0.6		1.3
			10	10		20
Q. stellata				1.3		0.6
				10		10
Prunus serotina				1.9		1.9
				20		30
Morus rubra						1.9
						20
Shrubs and Vines						
Tecoma radicans	389.4	243.8	88.8	240.6	30.0	78.1
	100	100	30	100	40	50
Rubus spp.	148.8	90.6	1.9	118.8		3.8
	80	80	20	90		20
Smilax glauca	25.6	0.6	1.3			5.6
	30	10	20			10

TABLE 4.—(Continued)

Age of stand	11	22	31	34	42	70–75
Rhus toxicodendron var. *radicans*	3.8	10.6	42.5	1.3	1.3	0.6
	10	10	50	10	10	10
Polycodium spp. (mostly *P. neglectum*	0.6	2.5	1.3	1.9		3.1
and *P. candicans*)	10	10	10	20		10
Crataegus uniflora and others	0.6	1.9	1.9	1.3	0.6	3.8
	10	30	20	20	10	20
Lonicera japonica		104.4	46.3			
		40	20			
Viburnum affine var. *hypomalacum*		6.3	23.8	53.8	4.4	42.5
		50	80	70	40	80
Parthenocissus quinquefolia		4.4	20.6			1.3
		20	60			10
Rosa virginiana		1.9				6.3
		10				20
Rhus glabra		1.3		1.9		
		10		20		
Rhus copallina		0.6	0.6	0.6		18.8
		30	10	20		20
Viburnum prunifolium		0.6	0.6	0.6		18.8
		10	10	10		20
Ascyrum hypericoides			1.9		0.6	
			10		10	
Viburnum rufidulum			1.3		1.9	9.4
			10		30	50
Amelanchier canadensis			1.3	1.9		2.5
			20	10		20
Evonymus americanus			0.6			2.5
			10			10
Viburnum acerifolium			0.6			
			10			
Vitis rotundifolia				2.5	1.3	3.8
				20	20	10
Ilex opaca					0.6	0.6
					10	10
Chionanthus virginica						1.9
						10
Herbs						
Cynodon dactylon	1500.0					
	30					
Andropogon spp.	837.5	27.5		40.0		20.0
	70	50		60		30
Solidago nemoralis	205.0		10.0	12.5	5.0	
	40		30	20	20	
Fragaria virginiana	120.0		7.5	20.0		
	40		10	30		
Solidago juncea	112.0			7.5	10.0	
	50			20	10	
Galium pilosum	95.0	52.5	10.0	10.0		10.0
	20	40	30	30		30
Cymnopogon ambiguus	50.0	2.5		15.0		
	30	10		20		
Chrysanthemum leucanthemum	40.0					
	40					

TABLE 4.—(Continued)

Age of stand	11	22	31	34	42	70–75
Eupatorium hyssopifolium	32.5	80.0	7.5	15.0	42.5	
	30	50	10	40	30	
Oxalis stricta	27.5	5.0				
	30	20				
Aster spp.	22.5					
	10					
Oenothera fruticosa	22.5				5.0	
	20				10	
Chimaphila maculata	17.5	192.5	190.0	25.0	22.5	57.5
	20	80	100	30	50	60
Physalis virginiana	15.0	5.0	2.5			
	40	10	10			
Solanum carolinense	15.0					
	30					
Erigeron ramosus	15.0					
	20					
Ipomoea sp.	15.0					
	10					
Cassia chamaecrista	10.0					
	30					
Diodia teres	7.5					
	20					
Pycnanthemum flexuosum	5.0			2.5		
	20			10		
Gnaphalium obtusifolium	5.0					
	10					
Prunella vulgaris	5.0					
	10					
Lespedeza repens	5.0	22.5	55.0	167.5	130.0	100.0
	10	30	30	90	50	70
Aster dumosus	2.5					
	10					
Scleria pauciflora	2.5					
	10					
Tragia nepetaefolia	2.5					
	10					
Polygala verticillata	2.5					
	10					
Hieracium venosum	2.5	2.5				
	10	10				
Daucus carota	2.5					
	10					
Rosettes (unknown)	2.5	40.0				
	10	50				
Taraxacum officinale	2.5			2.5		
	10			10		
Potentilla canadensis		132.5	20.0	55.0	5.0	37.5
		60	30	50	10	30
Desmodium obtusum		40.0			7.5	2.5
		40			20	10
Strophostyles umbellata		32.5				5.0
		40				10
Euphorbia corollata		20.0	2.5	47.5	45.0	7.5
		60	10	70	50	30

TABLE 4.—(Continued)

Age of stand	11	22	31	34	42	70–75
Galactia regularis		17.5	40.0	5.0	2.5	7.5
		20	40	10	10	20
Stylosanthes biflora		12.5		20.0		2.5
		10		20		10
Clitoria mariana		12.5				
		10				
Lespedeza sp.		12.5				
		10				
Viola sp.		2.5				
		10				
Desmodium nudiflorum			5.0		2.5	5.0
			10		10	10
Hieracium gronovii			5.0	5.0	5.0	5.0
			10	20	20	10
Prenanthes sp.				20.0		
				30		
Cunila origanoides				17.5		
				30		
Elephantopus tomentosus				17.5		2.5
				10		10
Eupatorium hyssopifolium				15.0		
				30		
Lobelia puberula				10.0		
				20		
Pycnanthemum pycnanthemoides				7.5		
				20		
Aster ericoides					2.5	2.5
					10	10
Lespedeza striata					2.5	
					10	
Desmodium canescens						10.0
						20
Desmodium sp.						5.0
						10
Sanicula marilandica						5.0
						10
Carex sp.						2.5
						10

that very few of these pine seedlings ever mature. Every stand has some of the seedlings present but individuals surviving more than one or two seasons become rarer as the stand matures. Should the stand be opened up by any cause these young plants are favored and they spring up rapidly, a few surviving in competition with the hardwoods which grow with them.

Represented among the counts of hardwood reproduction in the 11-year stand are *Liquidambar styraciflua* and *Acer rubrum*, species which predominate in the understory of older stands. In middle-aged stands these species with some black gum and less commonly tulip poplar may form a strong understory. Infrequently they may raise their crowns to the level of the overstory.

The density (8.8) of dogwood reproduction shows more individuals than

any other species except pine. Like the previously mentioned hardwoods, it becomes a characteristic understory tree and forms a stratum at a slightly lower level than red gum, etc. With it should be classed *Oxydendrum arboreum,* which occupies the same stratum as dogwood although usually present in somewhat smaller numbers. Like dogwood, its later appearance is already assured by the presence of its seedlings in the 11-year stand.

Of especial interest is the early appearance of seedlings (density 2.5) of black oak. An important element of the climax forest, it apparently may become established well in advance of its ultimate hardwood associates.

The status of *Juniperus virginiana* should be clarified and then perhaps it can be largely disregarded. In this vicinity, red cedar is the most ubiquitous of all woody species. Since it grows in every habitat and is associated with every plant community it can have no particular bearing on the trend of events. It appears along streams and on shady flood plains, on dry exposed bluffs, in pine woods, and in oak-hickory forest. Infrequently it may be the first tree pioneer in old fields. It is never a dominant, never a dependent and rarely in sufficient numbers to be of significance.

The shrubs and vines of the 11-year stand include *Tecoma radicans* and several species of Rubus. These two are carried over from the open fields and, under pine dominance, are here at their peak of development both as to numbers and uniformity of distribution. Reference to Table 4 shows that they are a part of this lesser stratum for many years but as stands mature they tend to decrease in numbers and to be more or less localized.

The other two shrubs *(Polycodium* spp. and *Crataegus uniflora)* and two vines *(Smilax glauca* and *Rhus toxicodendron)* are likewise species which, appearing early in the life of the stand, remain a part of it throughout its existence and are even found in mature oak-hickory forest.

Thirty-one herbs appear in the quadrat lists of this youngest stand. Of these about half are species regularly occurring in old fields. Their presence in the wooded area is easily explainable. Their low frequencies and relatively low densities indicate that they were localized. Observation shows that they are only present when small openings remain in the crown cover and when the canopy closes and shading becomes uniform, all are eliminated. Dense young stands have few of them but, if present, they disappear as the crown cover develops. Sixteen of these species do not appear again in the records for any of the older stands (Table 4).

Several perennials, important in the mature herb stages of old fields, are obviously less affected by shading and competition of the pine and its associates. Especially broomsedge, goldenrods, and *Eupatorium hyssopifolium* are only gradually eliminated as pine stands develop.

Herbs appearing almost simultaneously with pine and remaining as characteristic elements of the pine community are *Galium pilosum, Chimaphila maculata* and *Lespedeza repens.* It will be noted (Table 4) that, appearing

early in the life of the stand, these species rapidly increase in numbers and then drop off to a level which is maintained thereafter.

Twenty-two year Pine

Overstory.—At this age, distinct over and understories of pine have developed (Fig. 5). The total number of pine trees recorded is 27% less than in the 11-year stand but the number of vigorously growing overstory individuals is reduced by 32%. There is then a remarkably lower number of pines of tree size which must largely be the result of self thinning, a process which proceeds throughout the life of the stand but at a decelerated rate as the stand approaches middle age and maturity. The thinning is uniform, frequency of pine remaining at 100% until maturity. A single individual of *P. virginiana* appears in the overstory count. This is not unusual and yet it gives a mistaken picture for it was the only individual seen in the stand.

Understory.—At this age *Liquidambar styraciflua* is the most important understory species and with it are several hardwoods (black gum, sourwood, persimmon, dogwood, white ash) which typically remain understory indefinitely. Unless there is disturbance of some sort, this group of species does not become important in the overstory. Apparently the transition from pine to oak-hickory dominance does not affect the position of even such trees as red gum, white ash and black gum for they are also understory species in the mature upland hardwood forest.

Persimmon occurs regularly in young pine stands but decreases as the stands mature while white ash seems to be favored by the environmental changes associated with maturation of the stand. From this time on, dogwood, sourwood, and red bud, in the order of their importance, form a strong lower stratum in the understory.

In addition to these typically understory species, the appearance of hickory[4] is significant. The data from all more mature age classes of pine, show hickory present as an understory tree and that in general, individuals of tree size appear earlier than oak and are uniformly distributed. Later, oak reproduction must surpass hickory for in hardwood stands (Table 16) there are fewer hickory trees than oaks. Although hickory is slower growing and the number of seedlings is never great, a high percentage of them must survive to tree size.

Transgressives.—Reproduction counts in the 22-year stand show a marked increase over the previous age class, the total density advancing from 38.7 to 98.8. Whereas pine is the important species in the counts of previous stands, its percent of the total reproduction density here drops to a negligible figure (2.5%). The numbers of dogwood, red gum and red maple, all understory

4 Those who have attempted the identification of hickories in transgressive or seedling sizes, or even of mature trees without fruit know how impossible such a task becomes. The only solution in this work was to lump all species. The common upland hickories in the vicinity are *Carya carolinae-septentrionalis*, *C. alba* and *C. glabra*. Somewhat less common are *C. pallida* and *C. microcarpa*.

species, increase in the transgressive stratum and several such species (persimmon, red bud, sassafras, winged elm) are recorded for the first time.

At this age the oaks and hickories of the later overstory make their first conspicuous appearance on the forest floor. Though their individual frequencies are low, the four oaks (black, southern red, white, scarlet) appearing here, collectively make up 10.1% of the total reproduction and hickories comprise about 2%.

Whereas ten species are listed as making up the reproduction of the 11-year stand there are 17 species for the 22-year stand and, of these, nine are new. There is then a rapid increase in numbers of individuals during this early period of pine development, for reproduction densities more than double for the stands sampled. At the same time the number of species is also nearly doubled. The average frequency for all species shows an increase from 28% to 31% which is taken as an indication of a slight progression toward homogeneity.

Shrubs and vines.—As with the tree species, the number of shrubs and vines (13 species) is double that of the 11-year stand. Of the added species, winged and smooth sumachs might well have originated in open field although not present in the 11-year stand. Although common in field and roadside thickets they often maintain themselves throughout the life of pine stands in small numbers. The appearance of downy and cherry-leaved viburnum as well as Virginia creeper is indicative of true forest conditions, with shade and a stable forest floor. The viburnums increase in size and numbers as a stand matures and are an important element of the shrub stratum in the upland hardwood forest.

Lonicera japonica is an introduced vine which is spreading rapidly in this section. Most abundant in bottomlands, where it grows in rank tangled masses, it may also appear in upland woods. It may sprawl or climb, and often it reaches far up into tall trees. Where present in abundance it undoubtedly affects the development of species normally present. It develops to such an extent only rarely in upland pine woods, but locally it may be of some importance. Its bearing upon bottomland succession will be discussed elsewhere.

Herbs.—The species of sunny fields are eliminated or materially reduced in numbers before a pine stand is 22 years of age. Of the 31 species found in the 11-year stand, many of which had carried over from old fields, 15 did not appear in the 22-year stand or in any stand of greater age. Few of the old field species survive beyond this age.

Among the added species are *Potentilla canadensis, Euphorbia corollata,* and six legumes, *Desmodium obtusum, Strophostyles umbellata, Galactia regularis, Stylosanthes biflora, Clitoria mariana* and *Lespedeza* sp. Any or all of these may appear in older pine stands where the legumes often make up the major part of the herb stratum.

The greatest permanent change in herbaceous aspect takes place between 11 and 22 years for the data show fifteen species permanently eliminated during this period and nine species becoming established.

Thirty-one year Pine

Overstory.—Pine maintains dominance at this age with a frequency of 100% and a density of 15.1. This density is 17% less than that in the 22-year stand, whereas between 11 and 22 years pine density declines 32%. The

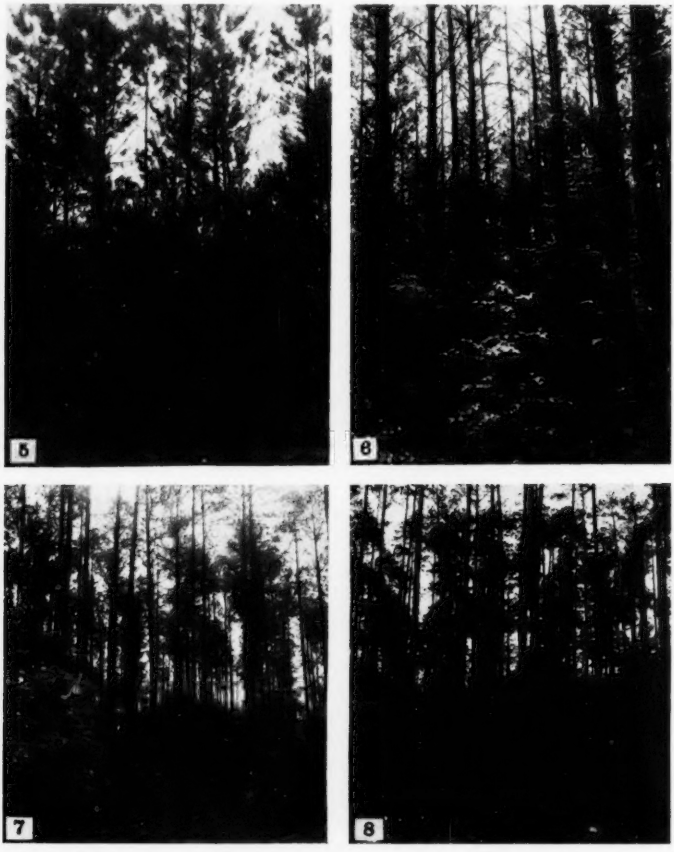


Fig. 5. Eighteen-year loblolly stand on upland field. Old field herbs still present, hardwoods barely established. Fig. 6. Twenty-six-year loblolly stand on upland field. Noticeable hardwood saplings are red gum, black gum, red maple and dogwood. Fig. 7. Forty-five-year loblolly stand on upland field. Hardwoods about same as in fig. 6 but now of tree size and forming an understory. Fig. 8. Seventy-five-year loblolly stand on upland field. Note degree to which pines have thinned and strong hardwood understory which here includes some oaks and hickory.

data for all stands suggest that the decline of pine density is most rapid during the first 15 to 20 years and then continues at a moderate rate through middle age and probably maturity.

White ash appears in the overstory record of this stand but in no others. Its constant occurrence in the understory of all stands with a low frequency and density supports the generalization that it is erratically present in upland pine forest but usually as a subordinate tree.

Understory.—All the hardwoods found in the understory of younger stands are again recorded here with only minor variations in numbers. *Acer rubrum* is an addition which in younger stands does not attain understory size. Typical, but rarely abundant in tree size, the species may be found in almost every mature pine stand. Black walnut too was added to the understory list. In all probability this species was more common here in earlier days but now it occurs only infrequently in pine and hardwood forests.

The complete absence of pine from the understory should be noted as an indication of the maturity of the stand. As a stand develops, the weaker understory pines, competing with shade tolerant hardwoods, are the first to be eliminated. As the stand matures only the dominant pines remain with none intermediate between them and the seedlings on the forest floor. It is this inability to maintain intermediate individuals which eventually eliminates pine as a dominant. When an understory pine dies or is removed by any cause, there are no pines to replace it and the deciduous species from the understory then grow up into the dominant stratum.

Transgressives.—The same species continue to reproduce under middle-aged pine stands for a considerable range of time. However, when counts are arranged in order of increasing age of stand, several trends become apparent. In general, all woody species except pine increase in density and the frequency values rise as well, indicating a more uniform distribution and an approach toward homogeneity. Reproduction of species of the understory such as dogwood, red gum and red maple appears first in relatively young stands and the numbers and distribution increase much more rapidly than do those of overstory species. These appear at later ages in small numbers which rise slowly although their distribution is soon uniform as indicated by high frequencies. The only species added to reproduction counts in middle-aged stands are those, mostly oaks and hickories, which eventually become a part of the upland hardwood forest. Northern red oak and black walnut seedlings were first recorded in the 31-year stand.

Shrubs and Vines.—As with transgressives, shrubs and vines show only minor changes at this age. The tabulation shows that practically all previously recorded species may be expected. Five additional species may occur *(Ascyrum hypericoides, Viburnum rufidulum, V. acerifolium, Amelanchier canadensis, Evonymus americanus)* all of which are typical of mature pine stands or hardwood forest. None of them ever appears in abundance nor are they to be expected in every stand.

Herbs.—At this age the composition of the herb layer has become fairly well stabilized and all species listed may be expected in middle-aged stands. Changes from the previous age class do not merit discussion other than the disappearance of a few shade intolerant species as *Clitoria mariana* and *Strophostyles umbellata.* The only added species are *Hieracium gronovii* and *Desmodium nudiflorum,* both characteristic of mature pine stands.

This 31-year stand represents a degree of middle-aged stabilization as to composition and appearance which is maintained for a number of years in all pine stands. The relative importance of subordinate species may change as the stand grows older but, in general, from this age on until hardwoods take over, the loblolly pine stand remains much the same in all strata from the dominant pine down to the herb layer.

Thirty-four year Pine

The gradual decrease in density of pine trees apparent in previous stands continues here even though the rather numerous understory pine had not been eliminated as rapidly in this stand as the previous one. This apparent indication of stand immaturity is contradicted by the presence of two southern red oaks and several red gums in the overstory. It is unusual to find hardwoods, especially oak, grown to overstory status in so young a pine stand.

The understory data are essentially as in the previous age class but southern red and post oak are added in the stratum and the presence of tulip poplar, which is typically a lowland species, also is indicated. Infrequent, and never in abundance, it is nevertheless not uncommonly present in the understory of midde-aged to mature pine stands on good sites. The presence of *Morus rubra* in the understory probably further indicates superior moisture conditions for it is characteristic of flood plains and bottomlands.

The tabulations of reproduction are scarcely different for the 34-year stand than the previous age. Post oak appears in the counts for the first time and thus the quota of upland oaks which grow on good sites is about complete. *Prunus serotina,* a minor associate in mature stands, also is first recorded for this age class.

Like all other strata the data for the shrub layer show no change except in the addition of *Vitis rotundifolia.* This grape is definitely associated with fairly mature stands, probably because of shade, moisture, or both. When well established it may cover the ground and climb high in the trees.

There is little to be said of the herbs. Certainly the slight variations from the previous age class are quite meaningless. However, five species are first recorded here which are restricted almost entirely to mature woods.

Forty-two year Pine

Trees.—This was an excellent pine stand which, at the time of sampling, appeared to be representative for its age (Fig. 7). Subsequent study of the data showed that conditions varied from the average sequence indicated by other stands. Investigations of the soil (Korstian and Coile, 1938) showed

that the area had at one time suffered serious sheet erosion although the forest floor, covered with pine needles, had all the appearance of a normal field. This may have resulted in a slowing down of vegetational development. The area could hardly be described as poor site for the pine had made normal growth. The principal differences were in the associated species. All hardwoods had apparently been slower to start than in most pine stands and were likewise slower to develop. Without the competition of hardwoods the pine made average growth and, at the same time, relatively fewer pine had been eliminated than in an average stand. Pine density was therefore relatively higher than would ordinarily be expected at this age. All understory pine had been eliminated but understory hardwoods which should thus have been favored were relatively small and present with lower densities and frequencies than in the 22-year stand. The list of species was similar to that of the 22-year pine except for the absence of ash and the addition of red maple and blackjack oak. Oaks and hickories should have been well represented in the understory at this age but the species were either absent entirely or small individuals were present with low densities and frequencies. Such retarded ecological development may often be related to poor site quality and this may have been a contributing factor here. However, the density of the pines suggests that the stand was probably considerably overstocked in its initiation and this, in itself, might have been sufficient cause for the later retarded development.

The lesser vegetation.—Reproduction in the stand reflected the conditions described above. Pine reproduction had a density (5.6) comparable to much younger stands (i.e., between 11 and 22 years) and the hardwoods all had densities much lower than expected at this age. The total number of stems on the transgressive quadrats was in the same magnitude as that of the 11-year pine stand although there were two more species present. Whereas the usual trend in developing pine stands shows a steady increase in transgressives with increasing age of stand, the average density per species in the 42-year stand was what could ordinarily be expected in a relatively young stand.

Shrubs and vines likewise were, for the age of the stand, low in numbers and species although *Ilex opaca*, more common in mature stands, was first recorded here. The list of herbaceous species as well as their numbers and distribution seem quite reasonable for an average pine stand of this age since the species present as well as their densities and frequencies fall rather logically between the 34- and 74-year records.

With such marked irregularities the data for this stand are out of place in an otherwise regular series. However, no usable stand of the same age class was found conveniently available and the data show that local variations in the rate of stand development do occur.

Seventy-five year Pine

Trees.—The first evidence of radical change in overstory appears in the data for this fine old stand (Fig. 8) in which many trees were overmature and all were approaching maturity. Under these conditions it would be expected that the pine population would be decreasing. The observed density

of pine at 11 years is 26.8, at 42 years 12.5, a 53% loss in 31 years. The next 33-year span represented by the 75-year stand shows a further reduction of 72% to a density of 3.4. This leaves only 12% as many pines as in the 11-year stand. That this elimination goes on evenly throughout the stand is shown by the constant frequency value of 100% in all stands except the last which, in spite of the low density, still has a pine frequency of 90%.

It might reasonably be supposed that, in so mature a stand, several hardwoods should be represented in the overstory. However, these old pines on average or good sites are very tall, much taller than the usual upland hardwood tree in this region. As a result, even at this age the pines still form an open overstory with the subdominant hardwoods making a second stratum beneath them. Below this subdominant layer is another stratum in which dogwood and sourwood predominate.

Transgressives.—Total reproduction counts are the highest recorded for any age although the species list includes only those found previously in younger stands. The high average density is related to the large numbers of dogwood seedlings and individuals produced by layering. Layering of dogwood does not become important under pine until the stand approaches maturity. It is a characteristic feature in hardwood stands. Exclusive of dogwood, slightly more than half of the count for woody reproduction is contributed by oaks and hickories. The number of species included is greater than for any other pine stand and viburnum (four species) is especially conspicuous because of relatively high densities. *Chionanthus virginica*, more often found in hardwood stands, is the only shrub species not previously listed in other age classes.

Herbs.—By this age herbs related to fields and open ground are almost completely eliminated but there are exceptions such as the Andropogon found in this stand as small isolated plants most of which had obviously just grown from seed. Apparently the herb population of the older pine stands becomes fairly well stabilized by the fortieth year for the species found in the 40 and 75 year stand are much the same with only minor variations in number of individuals.

e. *Shortleaf Pine (Pinus echinata)*

Billings' study (1938) of the development of shortleaf pine stands was thorough and his report is clear and complete. Since his methods of vegetational analysis followed the same pattern as those used in this study of loblolly pine and his report presents the same type of information in detail, it is possible to use his data and make direct comparisons of the ecological characteristics of the two types of stands. For these reasons it will suffice to say that the trends discussed for loblolly development are parallelel throughout the development of shortleaf stands with only minor variations.

f. *Virginia Pine (Pinus virginiana)*

The range of Virginia pine includes all of Piedmont North Carolina. In the lower Piedmont however, it occurs almost exclusively in mixed stands with

loblolly or shortleaf pine. Westward it increases in abundance and locally pure stands may be found in certain sections of the upper Piedmont. To the north in the Virginia Piedmont it is the predominating pine over wide areas. Nothing comparable to this development further north was observed in North Carolina although isolated stands of good quality were seen. This fact when combined with the difficulties of locating a successional series of comparable stands each undisturbed and extensive enough for phytosociological analysis served to discourage attempts at a detailed community study. Undoubtedly a usable series of stands could be located, especially in the northwestern Piedmont counties but, desirable as it might be for the completeness of this report, all present available information suggests that such a study would yield data more representative of the type if made somewhat further north.

Most Virginia pine stands in North Carolina appear less regular, in size and distribution of trees, than stands of the other pine species. Branches are slow to self-prune and this makes a well stocked young stand almost impenetrable. Lesser vegetation is retarded in the early stages of development of good stands and it would appear that this would likewise be true of the invasion of hardwoods. How this may affect the rate of succession to oak-hickory is problematical. Certain it is however, that within its range Virginia pine supersedes the broomsedge stage in old field succession, and as with the other pines, it is in turn succeeded by oak and hickory, the species varying with the site.

2. LOWLANDS

a. *Bottomland-pine communities*

The dissected topography of the Piedmont provides numerous depressions in most of which streams still flow. These bottomlands comprise a considerable portion of the total land area, but an individual depression is rarely very extensive. For the most part the streams are bordered by a relatively narrow flood plain beyond which there is a rather abrupt rise to the level of the surrounding terrain. Small tributary streams, often intermittent, lead into the larger streams from side valleys. The smaller lateral depressions, like the flood plains, provide quite different growing conditions than the uplands. Moisture conditions are here at their best and the soil, usually alluvial, is relatively rich and deep.

When extensive enough for cultivation, and accessible from the uplands, the stream margins have been cultivated and the majority still are. However, some are too wet, some flood too frequently and other reasons may cause abandonment. When these lowland fields lie several feet above the level of the present stream bed they are not subject to ordinary flooding and at the same time are relatively well drained. If cultivated for a number of years and cultivated well so that sucker sprouts have been eliminated, such fields may be clean and, at the time of abandonment, much like upland fields. When this is true, the trend of vegetational development may be similar to upland old field succession. The first years of weedy development are similar but plants are larger and more abundant. Preceding the appearance of Andropogon a dense

jungle of blackberries is characteristic. As a result, the broomsedge field of the upland does not appear here as a solid stand. After three or four years a variegated pattern of *Andropogon* spp. and *Rubus* spp.[5] may be anticipated. Assuming an adequate source of seed the Rubus-Andropogon stage may be superseded by pine.

Although the opportunity for observation is more limited for these than upland fields and conclusions therefore open to criticism it would appear that the bottomland pine stands are more commonly dominated by loblolly than by shortleaf pine. In fact young stands predominantly made up of loblolly were observed in bottomlands where the nearest source of seed was shortleaf pine.

Five bottomland pine stands were studied statistically, 15, 18, 34, 45, and 90 years respectively (Table 5). Each showed *P. taeda* as the dominant.

Fifteen-year pine.—Bottomland pine stands make excellent growth and it is not unusual for overstory trees to average five inches d.b.h. in fifteen years as they did in this stand. At this age the crowns form a closed cover which, however, is insufficient to have shaded out all vegetative evidence of old field origin. By fifteen years blackberries are usually dying out rapidly but their dead canes are always plentiful in young stands.

Stand maturation is more rapid than in uplands for by fifteen years there is a distinct understory developed. As indicated by this stand pines are most abundant (density 6.8) in the understory but red gum (0.4) and tulip poplar (0.5) are also present as well as winged elm (0.6), persimmon (0.8) and dogwood (0.1). As in the uplands red cedar is present in the understory of all lowland stands, increasing in numbers till about 34 years and then decreasing to almost nothing in the oldest stands. The size and early appearance of the hardwoods is particularly striking compared to upland stands.

Reproduction includes all the above hardwoods with red gum (29.4) and dogwood (22.5) most abundant but closely followed by winged elm (18.1) and red maple (18.1). The latter apparently starts a bit later than the other species for at this point it has not yet attained understory size. The early appearance of black oak is noteworthy as well as its consistent recurrence in the succeeding stands. This is the more interesting in that no tree-sized individuals of this species appeared in the plots in any stand. Birch, red and green ash, and sycamore are present in the transgressive strata in small numbers. These are typical bottomland hardwoods which play a more important role in another line of succession. The birch and sycamore especially are here really erratics. In pine succession the ash is potentially of some importance though it may remain an understory species indefinitely.

Among the shrubs and vines plants of Rubus are by far the most abundant. The density, 413.1, is based on living canes but dead canes far exceeded the

[5] No attempt was made to identify species of Rubus encountered in the quadrat studies. There are eight or possibly more species growing in the vicinity and some of these are rare or infrequent. *R. floridus* is apparently the commonest species carrying over from fields to pineland.

TABLE 5.—Density and frequency of trees in four size classes, and of shrubs, vines and herbs, in a successional series of five bottomland pine stands.

Age of Stand	15	18	34	45	90+
Overstory trees					
Pinus taeda	D 20.3	19.3	7.9	4.9	3.0
	F 100	100	100	100	90
P. echinata	D 2.1		0.3		0.6
	F 80		10		60
P. virginiana		1.3			
		50			
Liquidambar styraciflua			0.5	0.3	0.2
			30	20	20
Oxydendrum arboreum			0.1		0.3
			10		30
Liriodendron tulipifera					0.3
					30
Quercus borealis var. *maxima*					0.3
					30
Acer rubrum					0.2
					20
Juglans nigra					0.2
					10
Understory trees					
Pinus taeda	4.3	6.4	0.3		0.1
	100	90	30		10
P. echinata	2.5	0.4	1.9		
	80	20	60		
P. virginiana		2.5			
		80			
Liquidambar styraciflua	0.4	0.8	1.72	7.3	2.8
	40	30	100	90	90
Liriodendron tulipifera	0.5	2.0	1.0	1.4	0.4
	40	60	60	90	40
Oxydendrum arboreum			0.7	0.1	1.6
			40	10	80
Acer rubrum			1.6	4.4	6.8
			80	100	100
Quercus borealis var. *maxima*					0.9
					60
Juglans nigra					0.1
					10
Cornus florida	0.1	0.4	1.7	1.2	2.1
	10	30	70	70	70
Diospyros virginiana	0.8	0.1	0.1	0.1	
	30	10	10	10	
Ulmus alata	0.6				
	20				
Juniperus virginiana	0.2	0.2	1.0	0.8	0.1
	10	20	60	30	10
Sassafras officinale		0.2			0.1
		10			10
Cercis canadensis			0.5	0.2	0.3
			30	10	30
Prunus serotina			0.2		
			20		

TABLE 5.—(Continued)

Age of Stand	15	18	34	45	90+
Acer floridanum			0.1		0.8
			10		50
Ulmus americana			0.2	0.7	0.1
			20	40	10
U. fulva				0.2	
				10	
Morus rubra				0.2	0.8
				20	50
Alnus rugosa				0.1	
				10	
Carpinus caroliniana					0.5
					30
Ostrya virginiana					1.4
					40
Fagus grandifolia					0.5
					30
Fraxinus pennsylvanica var. *lanceolata*					1.0
					50
Carya alba					0.2
					20
Transgressives					
Pinus taeda		4.4			
		50			
P. echinata		2.5			
		30			
P. virginiana		3.8			
		30			
Liquidambar styraciflua	29.4	9.4	91.3	20.0	0.6
	100	70	90	100	10
Cornus florida	22.5	8.1	20.6	70.0	50.0
	90	60	60	80	100
Acer rubrum	18.1	18.8	25.6	35.6	156.3
	90	80	90	100	100
Ulmus alata	18.1	1.9			30.6
	90	30			70
Liriodendron tulipifera	6.3	52.5	1.9	1.3	
	60	100	30	20	
Diospyros virginiana	4.4	0.6	5.6	1.4	
	40	10	60	20	
Quercus velutina	3.1	3.8		3.1	13.1
	50	50		40	100
Betula nigra	1.9				
	10				
Morus rubra	0.6				3.1
	10				40
Fraxinus pennsylvanica var. *lanceolata*	0.6			0.6	3.1
	10			10	20
Juniperus virginiana	2.5	2.5	0.6		1.9
	20	30	10		30
Platanus occidentalis	0.6				
	10				
Carpinus caroliniana		6.9		2.5	16.9
		60		10	50
Carya spp.		5.0	7.5	11.9	56.3
		50	50	80	100

TABLE 5.—(Continued)

Age of Stand	15	18	34	45	90+
Quercus rubra		1.9			1.3
		20			20
Fraxinus pennsylvanica		1.3			12.5
		20			80
Quercus borealis var. *maxima*		1.3	1.3	1.9	11.3
		20	20	20	80
Oxydendrum arboreum		0.6	6.3		1.3
		10	30		20
Sassafras officinale		1.3	1.3	1.3	0.6
		20	20	10	10
Ostrya virginiana		0.6			53.8
		10			90
Celtis occidentalis		0.6			
		10			
Quercus alba			3.1	6.9	19.4
			40	50	80
Cercis canadensis			2.5		33.1
			20		80
Alnus rugosa			1.9	8.1	
			10	10	
Prunus serotina			1.3		4.4
			10		40
Quercus phellos			0.6		
			10		
Ulmus fulva				10.6	5.0
				50	40
Acer floridanum					16.9
					70
Nyssa sylvatica					5.0
					30
Fagus grandifolia					1.4
					20
Shrubs and Vines					
Rubus spp.	413.1	13.8	11.9	1.9	
	100	80	80	20	
Tecoma radicans	131.3	419.4	290.0	116.3	9.4
	100	100	100	100	30
Lonicera japonica	116.3	383.1	229.4	475.6	
	80	70	80	90	
Parthenocissus quinquefolia	11.9	1.9	80.0	173.1	63.1
	50	20	100	100	100
Viburnum affine var. *hypomalacum*	11.3	0.6	80.0	65.6	6.3
	50	10	100	100	50
Rhus copallina	2.5				
	10				
Vitis rotundifolia	1.9			3.8	5.6
	30			30	80
Rosa palustris	1.3				
	10				
Smilax (glauca?)	1.3	19.4	22.5	65.0	1.3
	10	10	90	80	10
Vitis labrusca	1.3			1.9	
	10			20	
Smilax rotundifolia		4.4			1.3
		30			10

TABLE 5.—(Continued)

Age of Stand	15	18	34	45	90+
Smilax bona-nox		1.9			0.6
		20			10
Polycodium neglectum and *P. stamineum*		1.3	3.1	4.4	2.5
		20	20	20	20
Ilex decidua		0.6			1.9
		10			20
Amelanchier canadensis			1.3		1.3
			20		10
Rhus toxicodendron var. *radicans*			3.8	61.9	17.5
			50	50	90
Evonymus americanus			3.1	16.9	13.8
			30	40	90
Cephalanthus occidentalis			13.1	3.8	
			60	20	
Vitis aestivalis			6.3		
			10		
Viburnum acerifolium			1.3	5.6	13.1
			10	30	50
Hamamelis virginiana				1.3	
				10	
Sambucus canadensis				0.6	
				10	
Viburnum rufidulum				2.5	
				20	
Ilex monticola				3.8	1.3
				10	10
Viburnum prunifolium					6.9
					50
Herbs					
Prunella vulgaris	75.0	25.0		5.0	
	50	20		10	
Panicum microcarpon	75.0				
	20				
Grasses (unknown)	50.0			5.0	62.5
	30			10	50
Ascyrum hypericoides	25.0				
	10				
Chimaphila maculata	20.0	5.0	7.5		
	20	10	20		
Oxalis stricta	20.0	10.0			
	40	30			
Solidago sp.	20.0		5.0	10.0	
	40		20	10	
Desmodium laevigatum	17.5				
	10				
Juncus effusus	17.5				
	40				
Strophostyles umbellata	12.5				
	10				
Hypericum punctatum	12.5				
	30				
Ambrosia artemisiifolia	10.0				
	20				
Potentilla canadensis	7.5	10.0	5.0	100.0	17.5
	10	10	10	60	20

TABLE 5.—(Continued)

Age of Stand	15	18	34	45	90+
Galium pilosum	7.5	57.5	5.0	32.5	5.0
	20	30	10	40	20
Lespedeza virginica	5.0				
	10				
Panicum sp.	5.0	7.5			
	10	10			
Polypremum procumbens	2.5				
	10				
Andropogon spp.	2.5	17.5	2.5		
	10	20	10		
Eupatorium hyssopifolium	5.0				
	10				
Antennaria sp.	2.5	12.5			
	10	20			
Gnaphalium obtusifolium	2.5				
	10				
Botrychium virginianum	2.5		2.5	5.0	
	10		10	10	
Galactia regularis		127.5			
		80			
Solidago juncea		92.5			
		20			
Cassia nictitans		65.0			
		50			
Chrysanthemum leucanthemum		50.0			
		40			
Panicum clandestinum		37.5			
		30			
Fragaria virginiana		30.0			
		30			
Diodia virginiana		27.5			
		30			
Eragrostis pectinacea		7.5			
		10			
Daucus carota		7.5			
		10			
Desmodium obtusum		5.0			
		10			
Acalypha gracilens		5.0			
		10			
Trichostema dichotomum		5.0			
		20			
Senecio aureus		2.5			
		10			
Ruellia caroliniensis		2.5		5.0	
		10		10	
Digitaria sanguinalis		2.5			
		10			
Hieracium gronovii		2.5	2.5	2.5	
		10	10	10	
Aristolochia serpentaria		2.5			
		10			
Corallorrhiza odontorhiza		2.5			5.0
		10			10
Scutellaria incana			5.0		50.0
			10		20

TABLE 5.—(Continued)

Age of Stand	15	18	34	45	90+
Oenothera fruticosa			5.0		
			20		
Salvia lyrata			2.5	5.0	
			10	20	
Smilacina racemosa				10.0	2.5
				30	10
Desmodium nudiflorum				10.0	5.0
				20	10
Rudbeckia laciniata				7.5	
				30	
Sanicula marilandica				7.5	12.5
				30	30
Lespedeza repens				5.0	
				10	
Cacalia atriplicifolia				2.5	
				10	
Asarum arifolium				2.5	
				10	
Hepatica americana					15.0
					20
Dioscorea villosa					5.0
					20
Viola sp.					5.0
					20
Elephantopus tomentosus					2.5
					10

living ones. Consideration of the succeeding age classes (Table 5) indicates an abrupt decline in numbers of blackberries between 15 and 18 years followed by a steady decline to complete elimination in mature stands. Next in importance are vines with *Tecoma radicans* and *Lonicera japonica* present in abundance and Virginia creeper, smilax and two grapes contributing to the tangled masses of vegetation. Downy viburnum is the only shrub of any importance. In the upland woods it does not attain such prominence until several years later.

The herbs include, in addition to those common in comparable upland stands, several species to be expected in lowlands or at least in moist soil, *Juncus effusus, Prunella vulgaris* and *Botrychium virginianum*. The difference between upland and lowland is further emphasized by the change in relative importance of certain species. Andropogon is far down the list with a density of only 2.5 and a scattered distribution. Other grasses, collectively, have much higher values while *Panuicum microcarpon* has a density far exceeding all species but *Prunella vulgaris*. Many other herbs of the 15-year lowland stand do not appear in the upland stands until they are much older, a probable further indication of better growing conditions in the lowlands as well as more rapid ecological maturation.

Eighteen-year pine.—The total tree population is not less at this age than three years before although the overstory shows a decrease of eight percent in density. Both red gum (0.8) and tulip poplar (2.0) increase in the understory.

The former tends to increase in numbers until the stand is middle-aged while the latter seems already to have reached its highest concentration at this point. Of the species which rarely, if ever, appear in the overstory dogwood increases steadily with the maturing stand but persimmon has its highest values in the 15-year stand and then declines to a low density and frequency.

Reproduction counts of species which were also present in the younger stand show no major variation except for the disproportionate numbers of tulip poplar seedlings (52.5). This is not the common condition but, in the vicinity of several seed trees after good seed years, such a crop of young tulip poplar may be expected. The saplings will be of even age, growing tall and close together. Self thinning may not begin for several years. New reproduction listed includes several typically bottomland species, *Carpinus caroliniana, Ostrya virginiana, Celtis occidentalis,* and *Fraxinus pennsylvanica.* Others which are less distinctive as to habitat but indicative of later developments in the dominant strata are the hickories, and southern and northern red oaks.

Between 15 and 18 years the density of *Rubus* spp. declines abruptly (from 413.1 to 13.8) which indicates the complete closing of the crown canopy and the assumption of dominance by pine in the three-year period represented. At the same time the growth of the lesser trees provides support for the climbing vines. Trumpet creeper and Japanese honeysuckle show enormous increases and two species of Smilax *(S. rotundifolia, S. bona-nox)* are added. As was true in this stand, these lianas may form a veritable jungle, festooning the trees, pulling over supple saplings and then growing up upon themselves in great piles.

The appearance of *Ilex decidua,* a typically subordinate bottomland species, is noteworthy. In old stands it attains the size of a well developed understory tree, often surpassing dogwood.

The herb list shows pronounced change over the 15-year stand. However, it represents merely another sample of a relatively young stand and gives little evidence of succession. Many of the species are still relicts of the old field and with three exceptions the eighteen species added in this stand do not appear in subsequent stands. *Hieracium gronovii* is typical of more mature pine stands, *Corallorrhiza odontorhiza* appears sporadically in any rich woods, and Ruellia does not have particular preferences. *Aristolochia serpentaria* rarely grows anywhere in abundance and it is so widely and irregularly spaced that it is not surprising to find it missing from the records for later stands. However, it is almost always present in damp or rich woods, most often a single plant at a time.

Thirty-four year pine.—During the 16-year period between this and the previous stand the overstory pine population is halved and red gum and sour wood attain the overstory. It is not uncommon for the latter to attain such size in the lowlands, and red gum is frequently a part of mature pine overstory though never abundant.

The understory records include *Acer rubrum* for the first time. Although starting more slowly it is from this time on as important as red gum in the

lowland stand. Eventually a few individuals attain the overstory but always later than red gum and tulip poplar.

Other subordinate trees of interest include *Acer floridanum* and *Ulmus americana*. It may be noted (Table 5) that red maple, elms and ash appear in the understory in gradually increasing numbers in each successively older stand but their density is never very high. Later it will be shown that this combination of species represents a stage in hardwood succession in bottomlands. Following pine, the stage never fully develops. Oaks, hard maple (noted above), beech and hickories, starting almost as early as the maple-elm-ash, are so far advanced when the pine stand finally opens up that they become dominant without this intermediate stage.

Transgressives are scarcely different than in the previous age class. Developmental trends are indicated by the increased importance of the subordinate species, dogwood and sourwood, and the understory species, red gum and red maple. Potential hardwood dominance is indicated by the increase in hickory and the first appearance of white and willow oak. The presence of *Alnus rugosa* in this and the next-aged stand, probably represents a relict condition, for the species occurs in wet bottoms as an early woody pioneer. Such clumps of alders within pine stands undoubtedly mark slowly filling old depressions or seepage areas.

Among the shrubs a continued decline in numbers of blackberries and a marked increase in downy viburnum indicate maturation of the stand with a closed crown cover and a stable forest floor. The absence of poison ivy up to this age is unexplainable. In mature stands it is always present, sometimes in great abundance and often growing far up into the trees, the main stem two to four inches in diameter. Also recorded are *Amelanchier canadensis, Evonymus americanus* and *Viburnum acerifolium* which are ordinarily not to be expected until the stand has attained some degree of maturity but thereafter are quite regularly present. Button bush, on the other hand, is far more common as a woody pioneer in wet meadows and other wet, semi-open ground. It seems unusual to have found it in a 34- and 45-year stand of pine.

The herb population in the 34-year stand seems to have arrived at a midpoint between the great numbers of individuals and species of younger stands and the appearance of species typical of the most mature stands. The species to be found in all pine stands are present, including *Chimaphila maculata, Galium pilosum, Hieracium gronovii,* etc. Andropogon, tenaciously persistent in upland stands, is not entirely eliminated in lowlands by this age although 32 other species present in younger stands are absent from the lists and do not appear in older stands. Only three species are added for the age class, two of which, *Scutellaria incana* and *Salvia lyrata,* may be expected here and there in the older pine stands. *Oenothera fruticosa* is far more common on roadsides and in fence rows than as an element of the woods flora.

Forty-five year pine.—The data for the 45-year stand (Fig. 9) are representative of lowland loblolly past middle age and approaching maturity. Density of overstory pine decreases about 38% as compared to the 34-year stand and no pines are recorded for the understory. Red gum density shows no

Fig. 9. Forty-five-year loblolly stand on lowland field. Rapid rate of ecological maturation here easily noticeable by comparison with fig. 7. Note size of red gum, density of understory, abundance of reproduction and ground cover. Fig. 10. Over-mature lowland loblolly (90 year) with extremely large but scattered pine and a well developed subdominant stratum of lowland hardwoods including oak, hickory, beech and hard maple. Lesser individuals include all these hardwoods in all size classes.

increase in the overstory as might be expected in a stand past middle age, for other hardwood species by then give serious competition.

In the understory, red gum and tulip poplar are at their peak for all stands, their numbers declining again as the stands approach maturity. Red maple, on the other hand, at this time is still increasing, for it tends to become more important in older stands and likewise carries over in the understory of the succeeding hardwoods. Slippery elm is first recorded here, as is red mulberry. The absence of mulberry from plots in younger stands is unusual for it is typically a bottomland species. Here too a single alder is recorded which, surviving competition, had grown to a small tree. As in the upland pine woods, dogwood forms a strong secondary stratum in the understory. This stratum is well formed by middle age and is maintained with slight variation throughout the life of the pine and into the hardwoods which follow.

Several trends in reproduction previously were discussed. However, the steady increase of all oak and hickory needs particular emphasis. At this age, they are collectively only exceeded by dogwood and red maple. Dogwood and red maple reproduction has a relatively high mortality whereas both oak and hickory have fairly high survivals. Oak-hickory reproduction increases 36% between 18 and 34 years and then 46% more between 34 and 45 years. The 90-year stand shows over 300% more oak-hickory reproduction than the 45-year stand. With good survival it is obvious what the probable result must be.

Shrubs and vines are much as described for the 34-year stand with tendencies toward decreases in several species of importance in young stands. *Hamamelis virginiana, Sambucus canadensis,* and *Ilex monticola,* which are to be expected in older bottomland forest, are first recorded here. All three are more apt to occur on stream banks.

The herb list too is similar to that of the previous stand with none of the species of young stands present except those which are found in all stands. In addition a new group of species appears, several of which are characteristic of mature forest with moist rich soils. Such are *Smilacina racemosa, Desmodium nudiflorum,* and *Sanicula marilandica.* These indicate the passing of the early stages of stand development when changes are rapid and radical and they mark the beginning of maturation in the stand with a relative degree of stability for some time to come.

Ninety-year pine.—This is the oldest known loblolly pine stand in the vicinity (Fig. 10). Being part of a tract along New Hope Creek which contains a summer camp explains its survival. The stand is overmature and, were it a part of a farm woodland, it would long since have been cut and destroyed. Of immense height and substantial diameter, several trees are 30 inches and more (d.b.h.) although the average is somewhat less. Here and there are the fallen trunks of individuals which have succumbed to disease or the elements. The size of these fallen trees makes them conspicuous and gives the impression that the stand cannot last much longer. However, during the 45-year period separating it from the previous stand the pine density declines by only 38%, essentially the same percentage rate of thinning obtaining between 34- and 45-year ages. Surprisingly the frequency is still at 90%. Perhaps the

rate of disappearance will be more rapid in the next succeeding period of years but a large number of the trees still look sound and it is probable that many years may be required to bring about hardwood dominance.

The opening of the pine crown cover serves to release several understory species which, as a group, share dominance with pine. Most conspicuous of these species are red gum, tulip poplar and northern red oak. However, it should be noted that, compared to the 45-year stand, red gum and tulip poplar are of less importance in the understory and much reduced in the reproductive strata while other species have increased. Red maple becomes the most important tree in the understory and with it a long list of species among which oak, hickory, hard maple and beech are significant in terms of succession. *Ostrya virginiana* and *Carpinus caroliniana*, well represented in the reproductive stratum of young stands, here appear in the understory. Both remain as subordinant but characteristic trees in mature lowland hardwoods. Dogwood has its maximum understory value at this age but, even so, its counts do not exceed those made under mature upland pine.

The total reproduction in the 90-year stand includes more individuals and species than any younger stand. Of this total reproduction, oak and hickory make up 20%, a definite increase over the 14% of the 45-year stand. The increase is the more significant because in this period there is a tripling of the total number of individuals of reproductive size. Two species appear which are not listed before. *Nyssa sylvatica*, so common in the upland stands, apparently does not thrive in pine stands on flood plains, at least not until they approach maturity. Sometime between 45 years and maturity beech becomes established, for several of transgressive size are recorded (density 1.4) and some individuals (0.5) have attained understory size. Seedlings and transgressives of *Acer floridanum* have a high density (16.9) and a wide (70%) distribution. However, observations indicate that it probably comes in considerably earlier than beech and that the high mortality of its reproduction reduces its potential importance. In spite of its earlier start and higher reproduction numbers the density of understory hard maple (0.8) at this age exceeds beech (0.5) but slightly. The combined reproduction of beech and maple comprises less than 4% of the total reproduction for the stand as compared to 20% for oaks and hickories. Studies of postclimax bottomland forest show that a similar proportion of oak-hickory to beech-maple is maintained when hardwoods become dominant.

Shrubs and vines are much as in middle-aged stands except for a marked decrease in numbers of the several lianas. Why this should be true is questionable. The absence of *Lonicera japonica* is undoubtedly a matter of chance. Here and there are lowlands to which this vine has not yet spread and apparently this stand had not yet been invaded. The appearance of *Viburnum prunifolium* is of interest since, like *Nyssa sylvatica* which also appears for the first time, it is common in upland pine woods.

The herbs are scarcely different from those of the middle-aged stand except for the addition of several more species characteristic of rich moist woods. These include *Dioscorea villosa, Hepatica americana*, and *Smilacina racemosa*. Undoubtedly these are further indicators of maturity. Only twelve species of

TABLE 6.—Ages of trees and the percentage of trees made up by each species in a series of miscellaneous bottomland pine stands arranged in the order of ages of pine at each station. REPR. indicates reproduction present.

Station	6	32	35	30	37	5	40	8	10	7	9	38–39
Pinus spp.	8–11	18	26	27	34–40	38–41	38–41	42	45	55	60	95–100
	100%	14%	6%	45%	60%	100%	30%	71%	19%	60%	13%	15%
Liquidambar styraciflua	REPR.	8–13	15–18	20	34	REPR.	35	36	4–9	38–50	22–35	30–75
		27%	56%	30%	20%		7%	14%	22%	40%	75%	5%
Liriodendron tulipifera		14–16		14	28	REPR.	25	38	8	REPR.	REPR.	20–46
		6%		15%	7%		4%	14%	3%			5%
Acer rubrum	REPR.	8–13	16	10	REPR.	REPR.	20	REPR.	3–5	REPR.	34	15–30
		38%	6%	5%			4%		9%		6%	21%
Fraxinus spp.		8	8–16		25	REPR.		REPR.	5	REPR.	REPR.	28–30
		3%	25%		7%				3%			5%
Ulmus spp.		6	8	18	14	REPR.		REPR.	3–7	REPR.	12	REPR.
		3%	13%	5%	7%				22%		6%	
Diospyros virginiana	REPR.	REPR.				REPR.						
Juniperus virginiana	REPR.					REPR.	10	REPR.		REPR.	REPR.	
							7%					
Celtis occidentalis						REPR.			REPR.	REPR.		
Carpinus caroliniana					REPR.		REPR.			REPR.		15
												10%
Morus rubra					REPR.			REPR.		REPR.	REPR.	10
												10%
Platanus occidentalis	REPR.	16–20										
		6%										
Cornus florida							8		7	REPR.	REPR.	20
							15%		3%			13%
Ostrya virginiana			REPR.		10							10–20
					7%							2%
Quercus phellos												20
												13%
Oxydendrum arboreum												24–45
												13%

herbs appear on the list and five of these are new for the series. The deeply shaded forest floor is suited to only a limited number of summer herbs.

Miscellaneous lowland pine stands.—The discussion of bottomland pine succession based upon quadrat studies could only deal with fully stocked stands which were extensive enough for the sampling technique employed. Bottomlands being what they are in the Piedmont region, the above detailed account may be misleading. Often stands are small and sometimes poorly stocked. There results a great variety of conditions not represented in the general discussion.

In Table 6 the ages of trees and their percentage of total stems are presented for several bottomland pine stands, each of a different age. These are again largely loblolly stands although in several instances shortleaf is an important component. Since there are no apparent vegetational differences associated with the two species, no distinction will be made.

The data are arranged in the order of ages of the dominant pines. Only a casual glance at the table shows the tremendous possible variation between stands. The deciduous species (red gum, tulip poplar, red maple, red and green ash, and elm) coming in under the pine are consistently the same, but their time of appearance, numbers and proportions are radically different. In some instances (stations 32 and 7) the stands are essentially mixed pine-hardwood for, although pine is slightly older, gum may come in very soon after pine is established. When as at station 32, the red gum and red maple continue to reproduce but pine as usual does not, a stand results in which uneven-aged hardwoods occupy the overstory with pine and make up a large percentage of the stems of tree size. This situation is presumed to be the result of poor seeding of pine in the first years of abandonment, resulting in an open stand which gives the hardwoods a distinct advantage as compared to normal pine succession. Stand 37 offers an interesting contrast, where the pine seeding continued for six years, indicating irregular stocking in early youth, but here hardwoods do not have the importance of the previous stands. The youngest pines are the same as the oldest red gum indicating that conditions favorable to the establishment of gum were paralleled by conditions checking the survival of pine seedlings. Station 35 illustrates a very open, understocked pine stand in which for some reason hardwoods do not seem to have gained as early an advantage. When they did, red gum, red and green ash, and red maple must all have appeared at about the same time.

Two overstocked stands are included (stations 5 and 10). Both represent dense, even-aged pine stands on excellent sites from which hardwoods have been successfully excluded for many years. The 41-year stand (station 5) illustrates a situation where no hardwoods are more than one inch in diameter or ten feet tall although reproduction of all expected species is exceptionally dense. The 45-year stand (station 10) is entirely comparable except that some of the hardwoods have grown above the reproductive strata to form a dense low understory of small trees. At station 7 red gum came in almost as soon as pine to form a dense pine-gum stand. Here again no other hardwoods have

progressed beyond the level of transgressives although 9 species are noted, most of which are present in abundance.

Herbs, shrubs, and vines show no irregularities peculiar to this series and need not be discussed. The data serve to emphasize the wide variation possible in bottomland pine communities. The generalization may not be entirely correct but apparently these irregularities are most frequently associated with narrow flood plains and small, patchy fields or plots which, at the time of abandonment, are surrounded by woods. Larger, open fields seem more apt to follow the regular line of pine succession.

DISCUSSION-SUMMARY OF PINELAND SUCCESSION

The statistics for pine communities of representative age-classes and as they occur in upland and lowland habitats have been presented in detail. There remain certain developmental characteristics in this major vegetation type which should be emphasized. Likewise there are several broad generalizations to be demonstrated as well as comparisons to be made between upland and lowland pine succession.

A discussion of dynamics in general, can best be accomplished after or with, graphic representation of the major vegetational changes. In Figure 11 phytographs are presented for all the stands studied in which loblolly pine played an important role. Arranged in chronological order, they present a summary of all data obtained in each stand and show the changes in the relative importance of pine as the stands mature. The data upon which the phytographs are based appear in Table 7. All individuals of the overstory and understory are included in the calculations. Density and basal area[6] of pine are expressed in per cent of totals for all species. Frequency, as given, is for pine only as are size classes which are represented in percent of the four strata distinguished in the counts.

The data for the 110-year stand apply to shortleaf pine and were transposed from the counts made by Billings (1938). Conditions in the two-pine types are very similar and it was desirable to have an overmature stand represented in the series. Since no information on loblolly of this age is available, it seems justifiable to insert these data here.

In the upland series, the irregularity of the 42-year stand becomes even more strikingly apparent than when considering the statistics. It is retained because it illustrates the degree of variation which may be expected resulting from different stocking or site quality.

Whereas the total numbers of pine decrease abruptly in the early years and then decline slowly thereafter (Tables 4 and 5), it is apparent that, in terms of total density for all species, percent of total tree density decreases much more steadily. Frequency of pine remains at 100% in both upland and lowland stands until middle age when the decrease in numbers of trees widens the spacing sufficiently to permit some quadrats to fall in areas without pine.

6 The cross sectional area at breast height. Determined by d.b.h. measurements of each tree and reference to standard basal area tables.

TABLE 7.—Data for phytographs of successional pine communities (Fig. 2).

Age of stand	% total density	frequency	% total basal area	% of four size classes
Upland loblolly				
11 years	100	100	100	25
22 years	65.3	100	96.3	75
31 years	51.5	100	97.8	75
34 years	36.8	100	88.3	100
42 years	76.6	100	98.1	75
75 years	22.1	90	93.8	50
110 years	6.6	80	88.0	50
Climax forest	1.5	3.3	0.7	100
Lowland loblolly				
15 years	91.8	100	98.8	50
18 years	89.0	100	98.5	100
34 years	29.5	100	87.7	50
45 years	22.4	100	63.8	25
90 years	14.5	90	75.7	25
Post climax	1.9	25	4.7	100

It is to be expected that the decrease in numbers and resulting wider spacing would continue, perhaps even more rapidly as the stands grow older, and that finally the number of pines would become of almost negligible importance.

All pines are not eliminated however. The phytographs for oak-hickory (Fig. 11) represent stands of uneven age in which many of the dominant trees are 250-300 years old. The species making up these upland and lowland oak-hickory stands are not the same. However, the phytographs showing the relationship of pine are remarkably similar for both. Evidently a few pine will remain as relics in any hardwood stand. These serve as seed trees and a few scattered seedlings may always be found. When, as frequently happens, an old deciduous dominant is removed by any cause, some pines will appear in the opening which results. Evidently some of these pines survive in spite of hardwood competition and a few pines of all sizes typically remain a part of a hardwood stand.

Total basal area of pine usually increases till beyond middle age even though total individuals are decreasing. This makes basal area a desirable measurement for it indicates something of size and importance of species when their numbers alone might be confusing. In the upland, pine still made up the major basal area (88%) of the stand at 110 years although its percent of total density was only 6.6% and frequency had fallen to 80%. The bottomland series showed a somewhat more rapid decline since basal area of pine fell to 64% in the 45-year stand and remained only slightly higher in the 90-year stand.

Whereas pine frequency does not decrease as rapidly in the bottomland stands, percent of total density and basal area fall off more rapidly than in upland pine forest. There are apparently more individuals of all species per unit area in the bottomland which perhaps results in slower growth for all species and a more rapid elimination of pine up to middle age. The greater producing capacity of the better site is likewise indicated.

The four size classes distinguished, included two strata of trees, over and understory, and two strata of transgressives. The latter were grouped as (1) seedlings less than one foot tall, and (2) transgressives over a foot tall to ten feet tall. Although further divisions could well be made, these four give a reasonable picture of the developmental relationships among the woody species present. Individuals under one foot are seedlings which may or may not survive. Those over one foot are saplings which usually are several years old and consequently have demonstrated their ability to develop and maintain themselves beyond the seedling stage. Understory individuals must, almost without exception, have originated in and grown up through the previous two stages. If for any reason the overstory or dominant stratum is removed, it may be assumed that these subdominants will then become the superior stratum.

The phytograph presentation of size classes is not completely satisfactory for it does not indicate which strata are represented. However, with a brief explanation the dynamic picture is enhanced by including these data.

In the youngest pine stands of average and uniform seeding, no dominant and subordinate strata can be recognized although individuals may have made

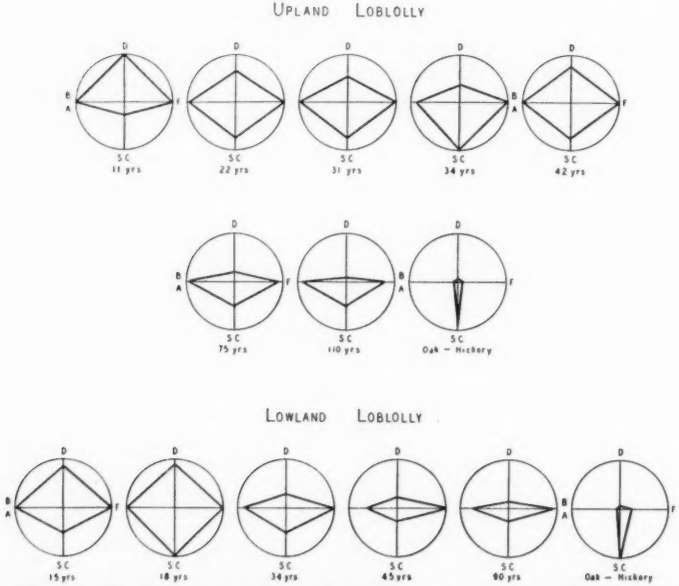


Fig. 11. Phytographs showing relative importance of pine to hardwoods in old field succession on uplands and lowlands. D—percent of total tree density, F—frequency present, SC—percent of four size classes (overstory, understory, transgressives, seedlings) in which the species occurs, BA—percent of total basal area. Zero is the center, 100 percent the periphery of the circle.

unequal growth. The 11-year upland stand is therefore given a value of 25%, indicating overstory. In a well-stocked stand seedlings would be rare. By 24 years the over and understory, are definitely formed and easily distinguished for many trees are making better growth and crowded or weaker individuals are being overtopped. Scattered seedlings appear on the forest floor accounting for the 75% size class representation. At 31 years the two tree strata are even more pronounced than before and the understory shows signs of thinning. As in the 31-year stand several trees are usually dead and many of the overtopped individuals look unhealthy. Seedlings are more frequent than in younger stands. The phytograph for the 34-year stand is similar to the previous one but 100% size classes are represented. This is the result of several pines surviving the seedling condition to become more than a foot tall. Apparently natural thinning of the tree sizes gives these seedlings some advantage at this stage. The phytographs for the older stands show that this is only a temporary condition for size classes drop to 50% and remain so. The 50% value in the older stands refers to overstory and seedlings.

This indicates that understory individuals either grow up into the overstory or are eliminated. Likewise the reproductive sizes, althought sometimes appearing in considerable numbers, survive only a few years and then die. Obviously some seeds germinate almost every year but the conditions of the forest floor are not favorable to their survival. In the upland oak-hickory stands all size classes are present although in relatively small numbers. It is obvious that so long as seedlings grow and representatives are present in all strata, pine will remain a part of the hardwood forest.

Reproduction in the bottomland pine stands shows an essentially similar trend but the changes appear to be telescoped in the earlier years. At 15 years, the two dominant strata are clearly distinguished so that the phytograph matches the 22-year condition in the upland. The 18- and 34-year lowland stands are equivalent to the 34- and 75-year upland stands in all characteristics measured. Apparently the 45-year lowland stand had already surpassed in ecological development, any upland stand studied. Not only had its seedling production ceased but basal area and density were also relatively lower. The 90-year phytograph indicates that this rapid maturation is followed by an extended period of slow change and mature bottomland hardwood shows a pine phytograph almost identical with that of the upland.

The above discussion and the phytographs emphasize pine and especially tree sizes. The indications of succession appearing in these data make it advisable to give some consideration to probable changes following pine. The only possible conclusion as to the next stage of development is that pine stands are succeeded by hardwoods in which oaks and hickories predominate. Later discussion of oak-hickory stands will show their variation and that, depending upon site, they have different species compositions.

Disregarding the species involved and lumping all oaks and hickories of tree size the data show a positive trend in the direction of oak-hickory dominance. Figure 12 shows the relative importance of pine and oak-hickory in

the successively older upland pine stands. Assuming a minimum age of 200 years for typical oak-hickory stands, the graphs shows a steady increase of oak and hickory in the dominant stratum while relative numbers of pine are decreasing. Again the density of the 42-year pine constitutes the only irregularity.

Successionally, the woody reproduction is a major indicator. The relationships of pine and oak-hickory with respect to density and frequency of reproduction as well as trees are shown in Fig. 13. Taken from upland pine data, the generalizations should however, apply to bottomland as well. The values used are absolute for the quadrats studied. The decline of pine tree density is matched by a slow, but persistent, increase in density and frequency of oak and hickory trees. When pine density has declined to a point where frequency falls below 90% the oak and hickory combination has developed a density exceeding the pine and a frequency of 100%.

Reproduction of pine is greatest in the youngest stand both as to frequency and density. Thereafter the 24-year stand shows an abrupt drop. It is apparent that the reproduction of the youngest stand must all have died and it may be concluded that, almost without exception, the seedlings live but a few years in all stands. Rarely are the seedlings more than two or three years of age and, when an occasional individual is older and a foot or more tall, it will invariably be weak and spindly. The abrupt decrease in size of the frequency-density block for pine (Fig. 13) between 11 and 24 years, undoubtedly represents the true state of affairs. As the figure shows, this drop is followed by a gradual rise and then a decline in numbers and distribution. The 42-year values are probably not true for the average series. Since the 34-year stand is the only one where transgressives taller than one foot are found, it is reasonable that the peak is somewhere near or following this age.

Oak and hickory of tree size appear as early as 24 years and thereafter show a slow but steady increase until the pine matures. At 110 years the oak and hickory approach the number and distribution of the stands in which they dominate. However, at 110 years they are quite definitely understory and pine still makes up 88% of the basal area.

The oak-hickory reproduction begins as early as in the 11-year stand and increases tremendously during the next 20 years. Thereafter it declines somewhat and probably maintains a fairly constant level until a strong hardwood understory is developed, then in the late stages of pine dominance the oak and hickory reproduction again increases although it does not approach that of a mature hardwood stand.

The steady increase in oak and hickory individuals of tree size indicates that a small percentage of the reproduction regularly survives the seedling stages, to become saplings and eventually appear in the understory. All the oak and hickory species are slow growing, and especially so when suppressed by a double canopy of pine and hardwood. The rapid increase of these species, both of reproduction and trees, when the pines thin out at maturity, is therefore not surprising. Many of these individuals which make up the count in the 110-year stand had been held suppressed for several years preceding.

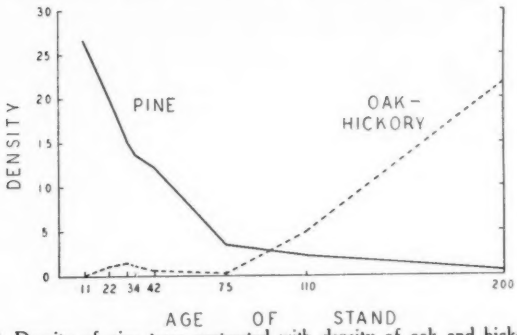


Fig. 12. Density of pine trees contrasted with density of oak and hickory trees in a successional series of old field stands of increasing age.

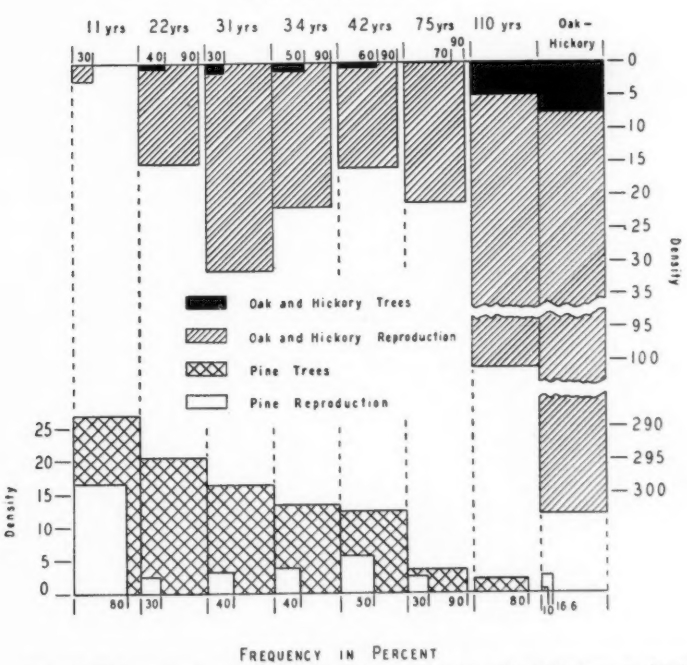


Fig. 13. Relationships of trees and reproduction of pine and oak-hickory as shown by their density and frequency in successive ages of pine dominance. Frequency is indicated by width of columns, density by height.

b. BOTTOMLAND HARDWOOD COMMUNITIES

The early stages of hardwood development in bottomlands are irregular successionally and stands may often vary within themselves. Slight differences in drainage or exposure may result in marked differences in stand composition, reproduction, associated herbs, etc.

Since bottomland hardwood stands are usually limited in extent and decidedly irregular in composition, the methods of sampling used for pine are not always possible. A detailed and logically intergrated statistical account cannot, therefore, be given. Whereas the pine successions are presented entirely from a statistical point of view and the discussion serves merely to clarify or explain the data, it now becomes necessary to make the presentation basically descriptive and interpolate statistical data when they are available.

All of the bottomland hardwoods are grouped into two forest types by Korstian and Maughan (1935), "red gum-yellow poplar" and "river birch-sycamore." The habitat of the former is designated as "moist, yet well-drained, bottomland" while the latter is said to occur "in narrow strips along the edges of creeks and rivers and in stands of small area in other moist situations." The concept of forest types is one of practicality, especially with relation to forestry practice and management. Since successional communities of the same series may be designated as types with equal rank it is obvious that community dynamics are not given major consideration in the classification. The relatively limited extent of the bottomland stands as well as the heterogeneity of stand composition make it impractical to recognize greater detail for general forestry purposes.

When these lowland stands are considered from an ecological viewpoint the two forest types are inadequate, if not actually misleading. Any, or all of the species named in the types may be found growing together in a single stand and any one of them may appear in pure stands as the dominant. When studied successionally, it becomes apparent that all of these species represent early stages of hardwood dominance in bottomlands and that the development of later stages is probably held in check by cutting and other treatments. Counts of reproduction and transgressives indicate potential communities dominated by tree species not even mentioned as characteristic of the bottomland forest types. Locally, where inaccessible, or in such restricted sites that they have escaped the axe, these species appear in small stands to corroborate the evidence found in reproduction counts.

The initiation of secondary hardwood succession in bottomlands may come about through various causes but the causes and resulting vegetational development are not always clearly related. Clear cutting, with no further treatment, results in stands of mixed hardwoods, the species being determined largely by the degree of successional development of the stand which was cut. In most instances, succession is advanced rather than retarded by the cutting for the resulting stand will be representative of more mature stages than the stand which was cut. Cutting followed by clearing and cultivation is usually restricted

to the better drained flood plains and when these are abandoned they develop along lines described under bottomland pine communities.

However, all cultivated bottomlands do not revert to pine, even though well drained, and the reasons are not apparent. Poorly drained floodplains, or even local depressions in potential pineland, regularly result in hardwood succession.

It is common practice to use cleared bottoms, too wet for cultivation, for hay land. These "meadows" may be found irregularly distributed along streams, completely surrounded by forest. Herb dominance is maintained only because of annual mowing. If left for only a year, woody species become conspicuous at once, probably growing from stumps as sucker sprouts. Button bush *(Cephalanthus occidentalis)* is regularly present and alder *(Alnus rugosa)* comes soon after. The latter often forms dense thickets, shoulder high or more, and it may take over an entire meadow.

The list of herbs making up the meadow vegetation is a long and, depending upon moisture, an irregular one. Sedges, rushes, and grasses are the dominants. Common grasses are *Andropogon ternarius, Panicum anceps, Sorghastrum nutans, Holcus lanatus, Anthoxanthum odoratum, Setaria geniculata, Triodia flava,* and several species of Paspalum *(P. laeve, P. circulare, P. floridanum)*. A long list of species of Carex is usually present as well as several species of Juncus. If the meadows are not mowed for a year, *Andropogon ternarius* tends to become dominant.

The wetter portions of the meadows always support *Juncus effusus* and *Carex lurida*. Frequently *Scirpus atrovirens* appears with them and less commonly species of Rynchospora. Several grasses appear rather constantly in the marshy areas. These include *Panicum stipitatum, P. clandestinum, P. microcarpon, Leersia oryzoides* and *Glyceria striata*.

The vernal aspect is colored by the abundance of Atamsco lily *(Zephyranthes atamasco)* which may be evenly distributed throughout the meadow. Meadows in the western portion of the region characteristically have a mixture of the Zephyranthes and *Castilleja coccinea* but in the lower Piedmont the latter is not present. The autumnal aspect, is marked by numerous composites, among which species of Solidago, Eupatorium (commonly including *E. perfoliatum*) and *Vernonia noveboracensis* are most conspicuous.

The exact trend of succession following abandonment of meadows cannot be given with certainty because there are several possibilities, depending upon site and especially moisture conditions. It is highly improbable that pine could ever be of importance. Pine seeds germinate most successfully in contact with mineral soil which is covered here by a grassy mat. In addition, conditions are favorable to hardwood germination and growth. No further discussion of meadows will be given specifically for, as in other situations, several types of vegetational development are possible.

The early secondary communities of bottomland succession are not clearly delimited from primary communities nor from each other. Within secondary

areas there are obvious situations which are essentially primary in nature. Such are depressions which are saturated or hold standing water for long periods and support only willows with alder thickets at the margins. Elsewhere, it would often appear that the entrance of different woody species and their maintenance was controlled by chance. The four major tree species, as indicated by the foresters types, may be found as pioneers in mixed stands in any combination and again, ages and size classes indicate that any one may be successional to another. Numerous observations under varying conditions, and age counts combined with records of reproduction and survival, do not bring out any definite trend.

Consideration of the data available on pure stands of different ages may clarify the relationships of the species.

(1) *Birch*

It is not uncommon to find birch lining the banks of streams in a narrow strip with all individuals of about the same age and size. Less commonly it may be found extending back from the stream and sometimes it occurs in pure stands over small areas. When occurring in pure stands away from the stream bank it appears that the situation may be considered as indicative of secondary succession.

Three stands dominated by birch were studied quantitatively. All were somewhat back from streams on level flood plains which had at one time been cultivated. Density and frequency for all species are shown in Tables 8 and 9. It cannot be said that these three stands are representative of all birch dominated communities but they appeared in comparable habitats and must be indicative of the development of such stands. In addition, certain inconsistencies in the data serve to emphasize the irregularities of vegetational development in bottomlands.

Six-year birch.—In the six-year stand many of the trees are ten to twelve feet tall and a definite overstory has formed. Birch is obviously the dominant for its frequency is 100% and its density (19.5) exceeds that of all other tree species combined. Sycamore ranks second in importance and scattered individuals of red gum, red maple and winged elm are also present. All species of the overstory are four to six years old but birch is most consistently six years and the others more often five and four years. The implication is that birch appears somewhat before these other species but another interpretation is possible. Since several of the others are also six years, it may be that at the time of its establishment birch had a better seed year or that conditions were more favorable for its germination and this resulted in its dominance. It does not follow that birch would have been dominant on this site regardless of the year of abandonment. For interpreting later successional phenomena it is important to note that sycamore, red gum and red maple all appear with birch. Ages of these species range from four to six years with six years predominating.

No well developed understory of tree size is recognizable. However, birch

TABLE 8.—Density and frequency values of tree species in three size classes for each of three ages of birch dominance in secondary succession.

Size Class		Overstory			Understory			Transgressives		
AGE OF STAND		6 YR.	14 YR.	36 YR.	6 YR.	14 YR.	36 YR.	6 YR.	14 YR.	36 YR.
Betula nigra	D	19.5	15.0	2.8		5.7	0.1	47.9	2.5	
	F	100	100	60		100	10	100	30	
Platanus occidentalis	D	7.6	0.4	0.5		0.6		27.1		
	F	60	20	30		50		80		
Liquidambar styraciflua	D	1.9		0.4		1.0	1.0	35.9	32.8	6.9
	F	20		20		60	40	100	90	40
Acer rubrum	D	1.3		0.1			1.5	22.7	58.3	13.8
	F	20		10			40	90	100	90
Ulmus alata	D	1.3		0.1			0.4	25.2	25.8	6.3
	F	20		10			20	80	80	50
Salix nigra			2.6			0.3		4.4		
			60			10		30		
Pinus taeda			0.4					1.9		
			30					30		
Liriodendron tulipifera			0.1			0.3		1.9	3.2	
			10			30		20	30	
Diospyros virginiana				0.5		0.2			8.2	
				20		10			50	
Ulmus americana				0.4			1.3			
				20			30			
Fraxinus pennsylvanica				0.1		0.1	0.8		0.6	
				10		10	30		10	
Alnus rugosa					1.3	1.2				
					20	30				
Cornus florida						0.1	0.3		6.3	8.8
						10	10		40	50
Carpinus caroliniana							1.3		1.3	
							40		10	
Morus rubra							0.6			3.1
							40			40
Fraxinus pennsylvanica var. *lanceolata*							0.1	1.3		10.0
							10	20		70
Juniperus virginiana							0.1		0.6	6.3
							10		10	50
Nyssa sylvatica								0.6		
								10		
Quercus phellos									1.9	
									20	
Q. rubra									0.6	
									10	
Carya sp.									0.6	
									10	
Quercus alba										0.6
										10
Aesculus neglecta var. *georgiana*										0.6
										10
Celtis occidentalis										1.9
										10
Ostrya virginiana										8.8
										40

TABLE 9.—Densities and frequencies of shrubs, vines and herbs in three age classes of birch dominance.

Shrubs and Vines		6 YR.	14 YR.	36 YR.
Rubus spp.	D	153.0	84.4	1.9
	F	100	100	20
Lonicera japonica	D	14.5	667.2	696.9
	F	20	90	100
Tecoma radicans	D	8.8	97.0	0.6
	F	40	80	10
Parthenocissus quinquefolia		1.3	89.5	93.8
		10	100	100
Vitis labrusca		0.6	1.9	3.8
		10	30	20
V. cordifolia		0.6	6.9	1.9
		10	10	10
Cephalanthus occidentalis		0.6	1.3	
		10	10	
Rhus copallina		1.9		
		10		
Viburnum affine var. *hypomalacum*			13.1	0.6
			70	10
Rhus toxicodendron var. *radicans*			10.6	128.5
			50	90
Smilax rotundifolia			7.5	18.1
			70	60
Bignonia capreolata			4.4	11.3
			30	90
Evonymus americanus			3.8	8.8
			30	60
Sambucus canadensis			0.6	3.1
			10	50
Smilax bona-nox				6.3
				40
Smilax glauca				6.3
				20
Viburnum rufidulum				5.6
				10
Rosa palustris				1.9
				10
Herbs				
Carex sp.		137.5	52.5	
		60	30	
Panicum microcarpon		132.5	80.0	
		80	60	
Potentilla canadensis		127.5		
		40		
Eupatorium hyssopifolium		120.0		
		90		
Juncus effusus		110.0		
		90		
Diodia virginiana		90.0		
		50		
Pluchea petiolata		75.0		
		20		
Boehmeria cylindrica		37.5	105.0	
		40	60	

TABLE 9.—(Continued)

Shrubs and Vines	6 YR.	14 YR.	36 YR.
Solidago spp.	32.5		20.0
	40		20
Hypericum mutilum	22.5		
	50		
Prunella vulgaris	22.5	137.5	110.0
	40	40	40
Lycopus virginicus	22.5	7.5	
	10	10	
Acalypha gracilens	20.0		
	30		
Andropogon sp.	20.0		
	30		
Eragrostis pectinacea	20.0		
	10		
Panicum scoparium	17.5		
	20		
P. anceps	15.0		
	10		
P. clandestinum	12.5	102.5	245.0
	20	90	60
Aster sp.	10.0	57.5	7.5
	20	50	10
Penthorum sedoides	10.0		
	20		
Polygonum sagittatum	10.0		
	10		
Strophostyles umbellata	7.5		
	20		
Juncus sp.	7.5		
	30		
Polygonum opelousanum	7.5	25.0	
	10	10	
Lobelia cardinalis	5.0		
	10		
Oenothera fruticosa	5.0		
	10		
Ambrosia artemisiifolia	5.0		
	20		
Galium pilosum	2.5		
	10		
Eupatorium album	2.5		
	10		
Impatiens biflora		60.0	0.3
		20	10
Fragaria virginiana		50.0	
		30	
Viola spp.		47.5	
		50	
Grass (unknown)		35.0	1.3
		20	20
Solanum carolinense		17.5	
		30	
Ranunculus hispidus		5.0	
		20	

TABLE 9.—(Continued)

Shrubs and Vines	6 YR.	14 YR.	36 YR.
Desmodium sp.		5.0	
		10	
Botrychium virginianum		2.5	
		10	
Oxalis stricta		2.5	
		10	
Verbena urticaefolia		2.5	
		10	
Ambrosia trifida		2.5	47.5
		10	20
Elephantopus tomentosus			2.5
			10

reproduction obviously continues for several years after the establishment of the first invaders for individuals less than ten feet tall, including seedlings, have a density of 47.9 and are uniformly distributed. Reproduction of other trees is made up largely of the species present in the overstory (Table 8) with red gum, sycamore, winged elm and red maple most important in the order named. In addition, there are scattered individuals of willow, tulip poplar, loblolly pine, ash and a very few black gum. The high proportion of birch reproduction indicates a continuance of birch dominance with the same species of the six-year overstory in association. However, the numbers of red gum which appear in the reproduction indicate its potential increase in the proportion of tree composition.

Eight species of shrubs and vines (Table 9) appear in the counts. Of these blackberry, winged sumac and buttonbush are common on open ground and, in older stands, would be expected to decrease rapidly. Sumach does not appear in the fourteen-year stand or later and buttonbush is not found in the older stand. The importance of blackberries in secondary bottomland succession has been emphasized in the discussion of pine. Obviously it is not restricted to pine succession for in this birch series it is still by far the most important shrub when birch is six years old. Thereafter it is rapidly reduced in numbers but not completely eliminated from the 36-year stand.

All the other woody species at six years are lianas typical of bottomland hardwoods. Their early establishment is of interest. All tend to increase in numbers and distribution as the stands mature.

Twenty-nine species of herbs are listed for the six-year stand (Table 9). Among these are the Andropogon and Ambrosia characteristic of abandoned fields, *Eupatorium album, Oenothera fruticosa, Potentilla canadensis,* and *Strophostyles umbellata,* more common along roadsides and other waste ground. *Eupatorium hyssopifolium,* in spite of its presence with a high frequency and density here, is also typical of upland pine woods as is *Galium pilosum. Eragrostis pectinacea,* which usually grows on dry and waste ground, seems peculiarly out of place. The other species on the list are all commonly known to grow in bottomlands or moist sites. Heading this list with high

frequencies and densities are *Juncus effusus, Panicum microcarpon,* and an unidentified Carex.

Fourteen-year birch.—Between six and fourteen years the total density of overstory individuals decreases from 31.6 to 18.5. This decrease is most apparent in the reduction of birch which drops from 81% of the total to 62%.

Some of the variation to be expected in bottomland hardwood is well illustrated. Red gum, red maple, and elm which make up a substantial portion of the tree layer in the six-year stand, are not present as trees here. Three other species take their places and, peculiarly, they include black willow and loblolly pine. Since willow is usually found in wet habitats and pine, when it appears, is found mostly in well drained bottoms, it is obvious that this occurrence must result from several poorly drained depressions with ridges between. Such conditions are most favorable to willow since its frequency is 60% and its density 2.6 as compared to 0.04 for pine. Further evidence of the irregularity in the habitat at the time of abandonment is found in the ages of the trees. The majority are thirteen and fourteen years but several willows are sixteen years, one birch is seventeen, and two pines are sixteen years. It would appear that for several years after abandonment there was a gradual change in drainage and soil moisture which became optimum for birch when the fourteen-year trees became established.

The six-year stand has no well distinguished over and understory of trees but the fourteen-year birch has these strata well developed. Total density of all individuals of tree size decreases during this short period from 31.6 to 28.0 and overstory density is only 18.5. This rapid thinning of the stand might be questioned but for the numbers of dead birch trees still standing. A count of dead trees gives a density of 14.5 and a frequency of 100%. The total density of living overstory and dead trees being 33.0, it is obvious that only recently the dominants had been quite comparable to the six-year stand. Understory willows are almost completely eliminated but those which keep pace with the overstory are only slightly affected. Since no new willows appear in reproduction it can be seen that they must soon be limited only to isolated individuals surviving in competition with longer lived and more aggressive species. Birch losses are likewise mainly from the weaker individuals of the understory. However, the number of understory birch remaining almost equals the dead trees and, since a few birch also appear in the reproduction counts, they should remain as important components of the stand for some time after willow disappears. Several ages are represented among the dead trees but some combination of conditions must have been particularly unfavorable three years preceding the counts, for about 80% of the birch and willow died in their eleventh year. Pine, like willow, shows its poor qualifications to compete in this environment for in this stand half the individuals of tree size had died and the scattered seedlings were rarely more than one year old.

Several species appear in the understory which invaded the habitat at a much later date than the birch overstory. These include sycamore, red gum, and tulip poplar all of which, in the six-year stand, started with birch. The appearance

of ash is successionally significant and dogwood indicates the beginning of a subordinate stratum. Persimmon is not uncommon in the early tree stages of secondary succession but is probably of little or no ecological significance.

Reproduction is of interest because of its successional implications. Young red maple, red gum, and winged elm are the most abundant and widespread while birch decreases to negligible numbers. Of understory species, dogwood, ironwood and red cedar appear. The reproduction and understory point to a potential new overstory, judging from observation elsewhere, with maple-elm-ash predominating and a lower stratum characterized by dogwood and ironwood. The appearance of red and willow oak and hickory is noteworthy for they are indicators of the final mature forest in bottomlands.

Shrubs and vines are so increased in numbers and species that they approach the distribution typical of mature bottomland hardwood. Blackberries and buttonbush are still present but reduced in numbers and quite obviously disappearing, as supported by the evidence from the 36-year stand. The lianas of the six-year stand are all present in increased numbers and distribution, especially *Lonicera japonica,* and three typical ones are added, smilax, poison ivy, and cross vine. Three added shrubs, downy viburnum, strawberry bush, and elderberry, are likewise characteristic bottomland species.

Of the 29 herb species found in the six-year stand only eight are recorded for the fourteen-year stand. These species remaining are typical of bottomland forest and may be expected regularly. Almost all have higher densities than in the six-year stand though frequencies are not increased materially. High frequencies are not to be expected for bottomland herbs since they tend to grow aggregated in colonies. This is especially true where Japanese honeysuckle is, as here, extremely abundant. Eleven new species are added among which are *Impatiens biflora, Ambrosia trifida,* and *Verbena urticaefolia,* all of which may have been carried over from earlier stages when they were abundant about the same wet depressions which still favor willow here. However, all may be found in older bottomland stands. The presence of *Viola* spp., *Botrychium virginianum* and *Ranunculus hispidus* is indicative of the stability of the forest floor and of the accumulation of organic debris.

Thirty-six-year birch.—This stand demonstrates that the apparent trends discussed for earlier age classes have continued. In the overstory, birch, which previously made up about 81%, now is reduced to 57% with a frequency of 60% and a density of 2.8. However, birch basal area far exceeds that of the other overstory species. Red gum and sycamore are again important associates as they are in the youngest stand. Slippery elm and persimmon also appear in the overstory although these two species are, in general, ten or more years younger than the birch. The ash and red maple of the overstory are usually no more than seven or eight years younger than birch.

The understory contributes to the same conclusions which can be drawn from above, namely, that birch and its associates are, by this age, well on their way out and that a new set of dominants is rapidly replacing them. Birch now

makes up only 1.3% of the understory while maple, elm, and ash together constitute 55%. Dogwood, ironwood, and red mulberry comprise about 27% of the understory and appear to be increasing, as they should, if a stand is approaching mature lowland forest.

Tree reproduction includes no birch or sycamore although the less sensitive red gum still germinates in reduced numbers (density 6.9). Red maple, green ash, and elm, together make up almost 50% of the total reproduction but of the reproduction of potential overstory species they comprise 78%. All evidence points to the development of maple-ash-elm dominance, which will be maintained for some time. The appearance of hop hornbeam reproduction is to be noted for it may become an important understory element in mature bottomland forest. Also present are buckeye and hackberry which are not uncommon in fairly mature bottoms but are not to be regularly expected. On the other hand, red mulberry is a characteristic species in rich lowland woods although never abundant.

The shrubs and vines include all lowland forest species previously recorded and an additional four new ones bring the total to sixteen species of which ten are lianas. It seems unusual that the open field *Rubus* spp. is not yet eliminated. The most important lianas are Japanese honeysuckle and Virginia creeper with frequencies of 100% which show their uniform distribution. The former is far more abundant with the surprising density of 696.9. Poison ivy and cross vine have frequencies of 90% and their relative importance seems reasonably indicated by their densities (128.5 and 11.3).

Even the high concentration of Japanese honeysuckle seems inadequate for explaining the remarkable decline in numbers and species (from 19 to 8) of herbs. This does not seem quite normal in terms of later observation elsewhere and may be a result of local conditions. The high density of *Panicum clandestinum* (245.0) is noteworthy as is that of *Prunella vulgaris* (110.0) which almost forms mats in places. Only *Elephantopus tomentosus* is added to the list of herbs.

(2) *Sycamore*

Several stands with sycamore dominance were located but their areas are either too small, or too irregular for detailed analysis by the methods used elsewhere, or for other reasons they are unsuited to the same type of quadrat work. The descriptions, therefore, must be somewhat more superficial.

Twenty-two-year sycamore.—This is the youngest stand available which is extensive enough to consider as representative of pure sycamore dominance. The site has unquestionably been cultivated, but during rainy seasons it must flood frequently for it is a low, level floodplain with rather poor drainage.

At this stage of development both over and understory are pure sycamore which forms a closed canopy (Fig. 14). The larger trees (12-20 in. d.b.h.) range from 19 to 22 years and lesser ages down to fourteen years are represented in the understory. About 60% of all the trees are 22 years old and the

numbers of younger individuals decrease as ages decrease. All sycamores are of tree size and not less than fourteen years old. There is no sycamore reproduction within the stand. It is apparent that conditions favorable to sycamore invasion existed for a relatively few years on this site and that here sycamore cannot maintain its dominance for long.

Reproduction counts indicate the probable trend of succession. Ash (both red and green) makes up 69% of the tree reproduction while elm (winged and American) follows with 12% and red gum, 8%. Red maple and birch each make up 3% and the ubiquitous red cedar, the remainder. These figures indicate an ash-elm-gum dominance to follow. However, red gum tends to thin out fairly rapidly in competition and, as in the birch series, it will probably decrease as maple increases in the maturing stand. Indications are that sycamore will yield to an ash-elm-red maple complex similar to that following birch although the reproduction of the three species suggests different proportions.

Other woody species incude a few blackberry canes, evidently relict of the early years after abandonment. In this same category are the scattered clumps of *Alnus rugosa, Sambucus canadensis* and *Cephalanthus occidentalis. Ilex decidua* and *Rosa palustris* are infrequently noted. As in most bottomland

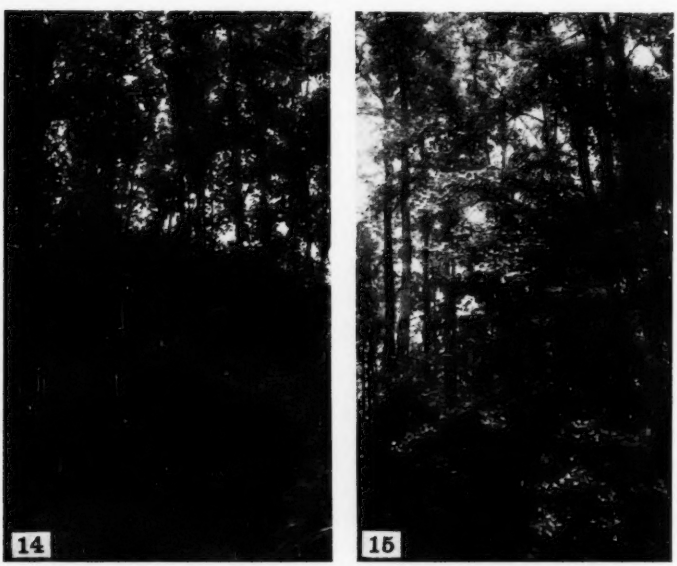


Fig. 14. Pure stand of sycamore under which is developing a dense community of red maple, American and winged elm, and ash. Fig. 15. Mature ash-elm-red maple forest on a rich flood plain.

forests, several woody vines are present in some abundance. These include *Rhus toxicodendron* var. *radicans, Vitis rotundifolia, Tecoma radicans* and *Parthenocissus quinquefolia. Lonicera japonica* is present but has not, as yet, attained the luxuriance so common in older moist woods.

Thirty-year sycamore.—This stand occupies a site comparable to the one just described but the dominants are only 60% sycamore which is largely between 25 and 30 years of age. A few younger sycamore trees are present but none are less than 15 years and there is no sycamore reproduction. Again, as in the 22-year stand, sycamore ceased to reproduce at a certain stage of stand development. In this older stand red gum (30%), ash (10%), tulip poplar (10%), and elm (5%) make up half of the individuals in the tree strata (over and understory). The ages of these trees indicate that they appeared as reproduction when the sycamore was between 8 and 15 years old but it is obvious that the stand remained pure sycamore for several more years since the other species have only recently begun to occupy a position in the overstory.

There is no sycamore reproduction and there has not been any for several years. Reproduction of other species is essentially as in the younger stand (22-year), although in somewhat different proportions. Elm (39%) and ash (23%) reproduction are again most abundant, gum and tulip poplars have both decreased to 8% and red maple is present in negligible numbers. Red mulberry is found rather generally (23%) and indicates its future presence. The appearance of elm and ash in the tree strata, their continued abundant reproduction and the decrease in red gum and tulip poplar are all indications of a stage to follow in which elm and ash will predominate.

The changes in proportions of species represented in reproduction may be related to the tremendous masses of Japanese honeysuckle which cover the ground and sprawl over anything able to give it support. Such a dense ground cover must have an effect upon germination and survival of young seedlings and observations indicate serious effects upon transgressives four to eight feet tall. Anything growing above the ground level of the mass of honeysuckle serves as a trellis upon which the liana soon climbs. The rate of growth of the honeysuckle is much more rapid than that of the tree and soon the mass of the vine bends the flexible sapling back toward the earth. The characteristic mounded effect of the massed honeysuckle is invariably produced in this way. Innumerable mounds were pulled apart in this stand and others, and always there was a dead or dying sapling beneath. Ash apparently suffers most from this form of elimination.

It would appear that honeysuckle has increased tremendously in this region during recent years and that its spread is still continuing. Its effects upon natural regeneration can only be surmised but there can be no question that successional trends in bottomlands are undergoing changes which are controlled by this introduced species.

In spite of the dense growth of honeysuckle in this stand it should be noted

TABLE 10.—Age and approximate percent of total trees for each tree species in a series of bottomland mixed hardwood stands ranging in age from eight to fifty-five years. The stations are arranged in order of increasing age and the upper of each pair of figures is the for individuals a species, the lower its percent of total trees in that stand. REPR. indicates reproduction.

Station	34	31	23	27	25–26	28	36	33	4	24	29	11–12
Willow	6–8	15	12				28	25–30		34		40
	100%	4%	38%				3%	2%		5%		1%
Birch			11–12	16–18	20–22	24		29	32	30–34	35	55
			51%	3%	1%	4%		1%	2%	19%	7%	1%
Sycamore		6–9	12	14	14	10–18		26	14	30	20–25	
		12%	2%	13%	1%	12%		1%	30%	10%	27%	
Red Gum	REPR.	9–10	REPR.	8–14	8–17	8–16	26	18–24	8–28	10–11	19–35	14–40
		71%		61%	59%	42%	24%	35%	43%	14%	13%	73%
Tulip poplar			5–6	12	12–14	15			22–24	25–28	14–20	25–33
			2%	2%	3%	15%			14%	5%	20%	7%
Ash (red and green)	REPR.	6–9		12–14	10–14	18	26	22–26	29–30	25–27	24	21
		12%		5%	11%	4%	67%	28%	14%	10%	7%	3%
Elm (winged and American)	REPR.		REPR.	8–12	10–14	15	19	18–24	30	20–30	10–18	10–35
				7%	8%	8%	3%	26%	7%	38%	13%	3%
Red Maple			REPR.	14	8–16		20	18–20	REPR.	REPR.	18	15–25
				2%	5%		3%	2%			7%	13%
Pine			12	18		20						
			5%	5%		15%						
Persimmon	REPR.		REPR.	REPR.				10				REPR.
								2%				
Ironwood		6						16			16	
		4%						1%			7%	
Willow Oak				6–14	14	REPR.		16		REPR.	REPR.	
				5%	3%			1%				
Red Cedar				6	REPR.	REPR.			REPR.			REPR.
				2%								
Red Mulberry				REPR.	14				REPR.	REPR.	REPR.	REPR.
					5%							
Flowering Dogwood					8					REPR.		REPR.
					1%							
Hackberry									REPR.			

that some ash and elm are outgrowing it to such an extent that they are gradually producing an understory.

Shrubs are few, probably because of the honeysuckle. Elderberry is the only species noted. The typical lianas are present, however, as before. Virginia creeper, muscadine grape, trumpet creeper, and poison ivy are all present but in smaller numbers than where honeysuckle is less abundant. The only herb recorded is *Boehmeria cylindrica* and it is not abundant.

Thirty-five-year sycamore.—Only slightly older than the previous stand, this one presents a different aspect. Sycamore is only slightly less abundant but, of all the trees present, the 30 to 35-year sycamores make up only 14%. As indicated by borings, red gum reproduction appeared when the stand was about 12 years old and continued to the present for a few individuals occur in the overstory and a strong understory grades into transgressives and lesser reproduction. Red gum makes up 43% of the trees but only a few are in the dominant stratum. Tulip poplar and ash, with all ages represented, each make up about 14% of the trees. Both are younger than sycamore. Elm is much less frequent (7%).

Reproduction supports the same trend indicated in the youngest sycamore stand. Ash (40%) remains the highest but it is closely followed by elm (35%), and red maple somewhat less (18%). The remaining reproduction is distributed among several species of which red gum (5%) is the most abundant. Hackberry, red mulberry, tulip poplar and hickory are also represented.

All of the shrubs appearing in the first two stands are also here and in addition cherry-leaved and downy viburnum are rather generally distributed. The same characteristic lianas are present, more conspicuous than in younger stands, except that Japanese honeysuckle is not as abundant.

Herbs are relatively much more numerous. In addition to *Boehmeria cylindrica,* several grasses and sedges occur, as well as clumps of *Redbeckia laciniata* and *Verbesina occidentalis*. *Impatiens biflora* is not uncommon; *Osmorhiza claytoni* is occasional; and violets are scattered everywhere. These are all species of mature bottomland hardwood forest.

This review of a series of sycamore stands demonstrates that, when undisturbed, sycamore may be expected to be followed by ash-elm-red maple. The reproduction in this series indicates that, when mature, these species may occur in this order of importance.

(3) *Bottomland Mixed Hardwood*

To interpret the ecological relationships of red gum and tulip poplar it would be desirable to have complete data from a series of pure stands of each. However, pure stands of either species are uncommon and a series of stands could not be located for study. The species frequently occur in combination, but uncommonly as dominants and rarely as single dominants. Very locally,

small patches of pure red gum or tulip poplar are seen but almost invariably these small areas prove to be minor variants of a more complex community since the surrounding habitat, similar in every way, supports a mixed stand of the same age class.

The mixed stands on areas of secondary succession in bottomlands are of irregular composition and do not readily fall into simply interpreted categories. Any one of several species may be present or absent and such inconsistencies do not appear to be related to differences in environment or age of the stands. A number of mixed stands were studied with respect to tree composition, ages of trees, reproduction and herbs. The only logical arrangement of these data seems to be by age of stand, regardless of dominants and their proportions.

Trees.—In Table 10 data for trees of fourteen mixed hardwood stands are arranged in the order of age of stand as determined by the oldest trees. Age and percent of total trees are given for each species in each stand. Obviously this is not a successional series in the sense that any one of these stands could be derived from a stand similar to any other. However, the tabulation should serve to clarify certain characteristics of bottomland hardwoods and especially to indicate the successional trend.

Certain species can be eliminated from the general discussion by a few preliminary remarks. Willow may or may not be present and its age is no positive indication of the time since abandonment. Its presence indicates that the habitat was once fairly wet or, more likely if it occurs in mixed hardwood, that locally there were wet depressions. If these depressions held water for long periods the willows may not have come in until sometime after other hardwoods became established on the better drained surrounding ground. This is not a common condition but, in terms of ages of trees, it eliminates a possible confusing element from consideration (see station 36 and 11-12). Ordinarily the widely dispersed seeds and rapid growth of willow facilitate its early establishment so that it becomes conspicuous before any other species make their appearance (station 34). This is probably also related to its ability to germinate in wet places and saturated soil. However, under other conditions, where soil moisture and drainage are better, willow may appear with the other species or very near the same time (station 23, 24). It will be noted that no willow is indicated for a number of stands. Here, it may be assumed that the local depressions favorable to willow had been eliminated by cultivation and that it had no opportunity to become established. Willow is then only an incidental species in secondary succession, its presence determined by special local conditions. It is rarely an important component of the bottomland stands except in early development. As the stands mature it is rapidly eliminated and the few individuals remaining in older stands are usually in poor condition and approaching death.

Pine may be considered as an incidental species in this series. Its presence is indicated in only three of the fourteen stands and then only in small numbers. Comparative ages indicate that it appeared on these sites with the

first tree seedlings. In the early development of the stands it is not uncommon for scattered pine to occur and for a few years it apparently withstands competition fairly well. However, as the hardwoods form a closed canopy the pine is rapidly eliminated as evidenced by the dead individuals recorded for several of the stands observed and its complete absence in the more mature stands.

That birch or sycamore may come in on lowland fields to form pure stands and then maintain their dominance has been shown. Here is evidence that both are likewise a part of the mixed bottomland hardwoods. Rarely making up a large percent of the trees, they are nevertheless so commonly present that they cannot be disregarded. Judging by age, birch appears somewhat before any of the other characteristic bottomland species although it does not precede willow. Ages of sycamore, in mixed stands, more nearly match the general age of other species.

There remain five typical bottomland hardwoods, red gum, tulip poplar, ash, elm, and red maple. Red gum is recorded in every stand but its density as well as percent of total density vary widely and inconsistently. Ages of individuals within a stand have a wide range and the time of appearance in the stand likewise varies considerably. All this should probably be expected, for red gum may be found in a great variety of habitats and conditions. In the bottoms it may appear as a pioneer tree, alone or with other species. Thereafter it maintains itself in competition and continues to reproduce for a surprising number of years (see stations 29 and 11-12). Of the species appearing early in bottomland succession it is least sensitive to environmental differences and best adapted to successful growth and competition under a variety of conditions. In spite of irregularities shown in Table 10, it is unquestionably the most important pioneer tree in the establishment of the mixed hardwoods in bottomlands.

Tulip poplar is not so generally present as red gum, being far more sensitive to habitat differences. Almost invariably it appears under other trees after a stand is well established. Typically it does not grow in boggy soil but on rather well drained areas. Its not uncommon appearance under mature pine on good upland sites indicates that its prevalence in bottomlands is not related to moisture alone. Although it becomes established later than other species it becomes an important tree in older stands. Its reproduction has a high survival, and exceptionally rapid growth soon brings it well into the overstory.

Acer negundo is not recorded for any of the stands studied. It is however, a member of this early mixed hardwood community. It ranges throughout the Piedmont but is only of local significance on wet flood plains in mixture with several other species.

Ash, elm, and red maple all make their conspicuous appearance (Fig. 15) somewhat later than the species already discussed and the ages recorded show that their appearance is, in general, in the order named. Of the three, red maple seems the least consistent in age as compared to age of the stand but regardless of stand composition it undoubtedly increases in numbers and

importance as the stand matures. The species of ash and elm are probably affected to a greater extent by site conditions and stand composition for their importance in the tree layers is irregular and unpredictable.

The remainder of the species recorded may largely be disregarded for they are never important components of bottomland forest, especially in these early stages of development. Individuals of tree size are recorded as they occur but the records for reproduction may be incomplete since they were not obtained on a quadrat basis. The repeated presence of persimmon reproduction is of interest since it is not typically a bottomland species. However, it may be found sporadically, especially in association with this mixed forest. Ironwood and red mulberry have been mentioned before as typical understory species in the well developed lowland forests and red cedar may be expected here as well as in any other habitat. Dogwood seedlings are probably present in more of the older stands than indicated, for, here as in the uplands, it forms its own stratum in stands which are approaching stability. Willow oak in these young stands is a secondary tree but in later development when oaks and hickories become dominant the willow oak becomes an important overstory species.

This phase of secondary bottomland succession is the most confusing of all trends on the forest. Those species which appear in pure stands can be placed in separate lines of development and conclusions drawn from their relationships are partially applicable to the mixed stands. In the latter, birch and sycamore tend to establish themselves earlier than other species. This may be an important factor in their ability to form pure stands. However, when their dominance is incomplete they are soon joined by red gum in rather high numbers and sometimes by tulip poplar which appears soon after the red gum. Ash, elm, and red maple, which follow pure stands of birch or sycamore as a distinct stage, here appear quite irregularly. Ash especially may appear as early as the gum, although not always, and elm and maple follow only a few years behind. For no apparent reason any one of the species may be absent from the mixed stands, except red gum which is aways present and usually makes up the highest proportion of the stand. As the stands develop, all the species continue to reproduce for some time although birch and sycamore are more apt to be even-aged. In the older stands birch and sycamore are, therefore, only represented by a few scattered relics. The continued reproduction results in an increased range of tree ages as the stands mature, with a closed canopy and a strong understory largely made up of the five major species. Their proportions are never the same and quite unpredictable.

Probably the mixed stand is of relatively long duration, perhaps 100 or possibly even 200 years. The nature of the reproduction in middle-aged stands as well as relict trees in postclimax bottomland forest indicate an eventual gradual change to oak-hickory dominance on these mixed hardwood sites.

Shrubs and Vines.—Quantitative data were not obtained for the lesser vegetation in this series. However, lists were made of the species observed in each stand. In Table 11 the woody species are tabulated to show the ages of

TABLE 11.—The occurrence of shrubs and vines in a series of bottomland mixed hardwood stands of different ages.

Age of stand	8	12	15	18	22	24	28	30	32	34	35	55
Alnus rugosa	×					×					×	
Rubus spp.	×	×	×						×		×	
Cephalanthus occidentalis	×			×	×							
Viburnum affine var. *hypomalacum*		×		×	×	×		×	×	×	×	×
Tecoma radicans		×		×	×	×		×	×	×	×	×
Parthenocissus quinquefolia		×		×	×	×	×		×	×	×	×
Vitis rotundifolia		×		×	×	×	×	×	×	×	×	×
Lonicera japonica		×			×	×	×		×	×	×	×
Smilax glauca		×	×	×		×	×	×			×	
Crataegus sp.			×									
Rhus toxicodendron var. *radicans*			×	×	×	×	×	×	×	×	×	×
Ilex decidua			×		×	×		×	×			
Viburnum nudum			×				×					
Samubucus canadensis			×		×	×	×			×	×	×
Rosa palustris				×	×	×		×	×			
Amelanchier canadensis				×								
Bignonia capreolata				×				×	×			
Sassafras officinale					×							
Ilex opaca					×							
Evonymus americana				×	×	×	×	×	×			×
Viburnum prunifolium					×	×			×			
Cercis canadensis									×			

stands in which they were found. Only the presence of the species is indicated with no attempt to evaluate abundance.

In the discussion of the tree strata it was shown that these stands are not all entirely comparable because of variable composition. It is not surprising, therefore, to find irregularities in the dependent species. The constancy of certain species is of especial interest.

The lianas (trumpet creeper, Virginia creeper, grape, Japanese honeysuckle, smilax, poison ivy) make their appearance very early in the development of the stand and thereafter may be expected in every age class, regardless of the dominants. Cross vine is the only exception and this cannot be explained for it is widely distributed in bottomland forests. Possibly it is more constantly present in still older stands than these which are available for study.

Shrub species, uniformly present, are downy viburnum and elderberry, while deciduous holly occurs somewhat less regularly. Strawberry bush is almost invariably present after the stand is well developed.

The first three species in the table (alder, blackberry, button bush) are more characteristic of open ground. Their irregular occurrence in the stands indicates that they are gradually eliminated but that the rate of elimination varies tremendously in different stands. The several other species listed (shadbush, sassafras, redbud, etc.) are not restricted to bottomlands and their irregular appearance here suggests that, in the earlier years of mixed hardwood succession, they are merely incidental.

TABLE 12.—The occurrence of herbs in a series of bottomland mixed hardwood stands of different ages.

Age of stand	8	12	15	18	22	24	28	29	32	34	35	55
Vernonia noveboracensis	×											
Eupatorium aromaticum	×											
Juncus effusus	×											
Juncus sp.	×											
Carex spp.	×		×	×	×		×		×			
Grasses (unknown)	×		×						×			×
Viola spp.	×	×	×	×	×			×	×	×		×
Aster laevis		×										
Ambrosia trifida		×	×									
Tiarella cordifolia		×					×					
Agrimonia parviflora		×			×		×	×				
Boehmeria cylindrica		×			×	×	×	×	×	×		×
Impatiens biflora		×	×	×	×	×	×	×	×	×	×	×
Hypericum punctatum			×									
Galium aparine			×									
Geum canadense			×	×			×	×				
Solidago sp.			×						×			
Verbesina occidentalis			×	×	×				×			
Solanium nigrum				×								
Ruellia caroliniensis				×	×							
Asplenium platyneuron					×							
Chimaphila maculata					×							
Epigaea repens					×							
Potentilla canadensis					×							
Elephantopus tomentosus					×							
Botrychium virginianum					×			×				
Prunella vulgaris					×			×				
Zizia aurea					×		×	×				
Verbena urticaefolia					×						×	
Saururus cernuus					×			×				×
Phryma leptostachya					×							×
Carex hystericina						×						
Onoclea sensibilis							×					
Hypericum mutilum								×				
Ranunculus hispidus								×				
Ranunculus abortivus								×				
Osmorhiza claytoni									×			
Rumex conglomeratus									×			
Rudbeckia laciniata									×		×	
Equisetum praealtum												×

Herbs.—The tabulation of occurrence of herbs (Table 12) in bottomland hardwoods serves to emphasize the variation in these stands as to origin, drainage, rate of development, etc. The species in the eight-year stand could all have been carried over from the first years of abandonment and they indicate a fairly moist or even poorly drained field. The herb list of the 22-year stand shows some similarities to much more mature possibly subclimax, forest. In all probability this area is well drained and rarely flooded or this combination of herbs could not be present. For some sites only a few herbs are noted. This is ordinarily unusual in bottomlands but when *Lonicera japonica* becomes abundant in a stand few herbs can survive.

Herbs on the list which may regularly be expected in bottomland hardwoods include several species of Carex and Viola as well as a variety of grasses. The species of the latter occur with no great degree of constancy. *Impatiens biflora* and *Boehmeria cylindrica* are both shade loving species of moist habitats and hence regular members of hardwood bottomland communities. *Agrimonia parviflora* and *Geum canadense* are in much the same category, but apparently they are less tolerant of a variety of conditions and consequently not as generally present. *Saururus cernuus* is a certain indicator of poorly drained depressions which remain saturated for long periods. *Solanum nigrum* and possibly *Potentilla canadensis* may be considered as ubiquitous weeds of fields or roadsides, otherwise this list is rather typical of what may be found in bottomland forest. The constancy with which certain species appear in stands of different ages is probably not unreasonably represented in this series.

SUMMARY OF SECONDARY LOWLAND COMMUNITIES

Slight variations in topography and drainage have pronounced effects upon moisture conditions in bottomlands. These effects are reflected in the vegetational development which, as a consequence, may have several different expressions in a single flood plain. Bottomland communities are therefore often made up of mixtures of species whose relationships are decidedly confusing. Only the major trends of development are summarized here.

Some of the species occasionally occur in pure stands where their habitat preferences may be suggested and their relationships to other species may be indicated. On the basis of these pure stands certain trends may be recognized.

Well-drained, fairly extensive floodplains almost invariably have been cultivated. When abandoned they are usually occupied by pine stands whose development is comparable to, though more rapid than, upland pine.

Hardwoods are favored by sites which are moister or less perfectly drained than the pine sites. Mixed hardwood stands, made up of several species, are the usual dominants. However, under exceptional circumstances which probably involve favorable seed years and particular conditions for germination, birch or sycamore may be the pioneer tree species and form pure stands. Neither continues to reproduce abundantly in its own shade for long. The understory is invariably a mixture of species among which red gum and tulip poplar predominate in younger stands. These two species tend to form an important part of the dominant stratum by middle-age. At that time or soon after, red maple, elm (winged and American) and ash (red and green) in varying proportions, are most important in the understory and with increasing age they tend to become dominant.

If conditions are not favorable to the establishment of pure stands of sycamore or birch, the pioneer tree community may be made up of a mixture of any or all of the species mentioned. Again the trend is toward red gum dominance by middle age, with or without tulip poplar associated. As before, this phase is followed by some combination of red maple-elm-ash dominance (Fig. 15).

Regardless of early variation, all evidence indicates eventual maple-elm-ash dominance. The ultimate lowland community of oak-hickory (postclimax) is today found only locally. This is discussed later.

B. FIRE

In spite of long-time records which indicate adequate rainfall in the Piedmont and a rather even distribution of precipitation throughout the year, there are frequent periods of drought. These dry spells may come at any time but are most common in late summer and fall while temperatures are still high. Under these conditions the accumulated forest litter, especially under pine stands, constitutes a serious fire hazard.

State and county agencies have, in recent years, done much to reduce fire losses through education as well as fire patrols but the practice of burning pasturage and brush is still general and often done in a careless manner. Hikers, fishermen, automobile drivers and others are likewise often thoughtlessly responsible for starting fires in unexpected places. A combination of circumstances may keep fire damage at a low level in the region. Vigilant policing may check many fires before they have reached serious proportions. This is often possible because of the tendency for fire to sweep along the ground in middle aged pine stands, where ground cover is slight and understory trees and shrubs are relatively few. Again, individual stands are usually not large and the agricultural nature of the territory results in a patchwork design of cultivated and forested land. Fire is much more easily checked under such conditions than in extensive stands of uniform forest.

A comprehensive discussion of the effects of fire on succession and development of stands might well be included in a report such as this. However, the subject is too broad and information as yet too limited to pretend any approach to completeness. No detailed studies were made except of an area being periodically burned under control as an experimental phase of another problem. Enough information is available to justify a few generalizations regarding successional trends.

The effects of ground fire are variable depending upon such conditions as age of stand, intensity of burning, and time of year. Young pine stands undoubtedly suffer more severe injury than older stands which have developed stratification. In the older stands a ground fire leaves the tree stratum intact and only the shrubs and transgressives are injured. Numerous areas of this type were observed and, several years after a fire, the only marked evidence of burning is the fire-scarred trunks of the trees. In spite of the apparent similarity of lesser vegetation however, stands which are seen before and after fire show a marked set-back in the subordinate strata. Judging by the few stands which had been studied previous to ground fire the lesser woody vegetation suffers remarkably little except that it is smaller in size than in unburned stands. From limited observations it would appear that oak and hickory reproduction is reduced only about 50% since many individuals apparently sprout from the roots. The associated species such as red maple and dogwood may be

more radically reduced for losses of 60 to 75% were observed. In these same stands *Nyssa sylvatica* doubles its numbers and persimmon appears in some abundance although absent before fire. The only shrub seriously affected is downy viburnum which is reduced more than 80%. All other shrubs and vines remain essentially as before except that *Rosa virginiana* is added to the lists after fire. Herbs show remarkably little difference in numbers of individuals but the number of species is increased by several common annual weeds typical of open ground.

It is probable that a ground fire does not materially affect a well developed pine stand floristically and, therefore, its effect on succession is merely to reduce the rate without changing the trend. The effects of several successive ground fires in the same stand would probably be much more pronounced.

When fire sweeps an entire stand and reaches the crowns of the overstory pine the result is quite different. An occasional pine may survive but the area will, in general, be swept clean of vegetation leaving scattered charred trunks standing, and partially burned logs in a tangle as they have fallen.

The revegetation of an area so intensely burned is rapid and the trend of development is largely determined by the nature of the stand preceding the fire. The first year's growth is largely herbaceous with species characteristic of open fields predominating. Andropogon is conspicuous (especially *A. scoparius*) and the composites of roadsides and waste ground are numerous. In addition any of the herbs found in pine stands may be found. *Rubus* spp. soon become abundantly established resulting in a low jungle of blackberries and herbs with a great mixture of species.

The hardwoods which were present in the pine stand, like the pine, will have been burned to ground level but, unlike the pine, many of the hardwood stumps survive and their sucker sprouts soon appear above the herb stratum. Most conspicuous of these species are red maple, red gum and, to a lesser extent, dogwood and ash. Winged sumach is apt to be locally abundant and sometimes sassafras. Certain species may appear from seed in rather large numbers and make surprisingly rapid growth. These include red gum and ash but black cherry, tulip poplar and red bud are apt to be most frequent. In spite of the rather dense cover of herbs and hardwoods numerous pine seedlings appear and survive. These make rapid growth so that mixed pine-hardwood is not uncommon in younger stands on burned-over areas. Pure pine stands have not been observed and are not to be expected.

C. CUTTING

A systematic survey of vegetational changes following cutting is beyond the scope of this report but a few generalizations may not be out of place.

Thinning in young pine stands does not affect the floristics of the stands. It serves to reduce competition and thus brings the remaining trees to merchantable size in a relatively shorter time than when natural growth is permitted. Most of the trees removed would, in time, have been eliminated by natural

causes and so the thinning really speeds the processes involved in succession. Selective cutting in mature pine stands produces the same ecological end but the results are noticeable sooner. Inevitably it must result in a mixed pine-hardwood condition which will eventually become pure hardwood. Gradual removal of the pines will release the associated understory hardwoods such as red gum, tulip poplar, and red maple, and these species will become the important components of the stand. Continued selective cutting should, according to ecological observations, result in a gradual increase in such hardwoods as oaks and hickories, the species varying somewhat with site.

Clear cutting represents an extreme of treatment that is not uncommonly practiced. Strip and spot cutting are still in the experimental stage but, depending upon site and seed source, may probably be advantageously used to modify or control the composition of second growth stands. Clear cut areas are sometimes turned to pasture or, more often, burned and cleared for cultivation. When cutover land is left to recover without further interference the development of vegetation is variable from site to site but, in general, so similar to fire succession that discussion is scarcely necessary. To be sure, recovery of the stand is probably more rapid than after fire and undoubtedly fewer new species are introduced which were not associated with the parent pine stand. However, a mixed hardwood stand may be anticipated, made up largely of the fast growing hardwoods which were associated with the pine and which will to a large extent be derived from sucker sprouts. A scattering of pine derived from seed is not unusual. As in all secondary succession of this type, the maturation of the stand will result in changes tending toward hardwood climax and, in spite of the cutting, the approach to the climax will probably be more rapid than had the stand never been cut.

Mature hardwood stands are too few and too infrequently affected to permit generalizations on changes following their burning or cutting.

From an ecological point of view it is obvious that, without artificial assistance such as cleaning, an area from which all pine has been removed by fire or cutting will, under natural conditions, come back to hardwoods. A hardwood stand reduced to ground level will likewise produce hardwoods. In both instances the effect will be to bring the resulting stand much nearer to oak-hickory dominance than the parent stand which was destroyed.

II. Primary Communities

The preceding discussion deals only with those communities which represent phases of the revegetation of areas upon which plants have previously grown. All these communities are the result of disturbances of some sort, especially man's activities such as cutting timber and clearing and cultivating fields. In the normal course of events a long and relatively completely populated area such as the Piedmont could not avoid rather complete exploitation along these lines and, as a result, secondary communities comprise the bulk of the vegetation.

Locally, on restricted areas, are communities which are invading or developing in habitats quite unrelated to man's activities. Either these habitats are

newly formed and support pioneer vegetation for the first time, or, for various reasons, man has not found it expedient to tamper seriously with the natural development of the community. Such undisturbed habitats as well as the successions of vegetation upon them are termed primary. It is obvious that these areas and their vegetation can be of little economic importance but ecologically they may be of great significance for from them may come valuable clues to the vegetational trends before the extensive influence of man. Within these isolated areas may be the remnants of once widespread species now remaining only as relicts. Approaching the limits of the range of a species it can rarely compete with the usually aggressive members of secondary communities and, if present, will most frequently be found localized in the more stable, vegetationally mature primary areas. Those primary areas where succession is still in its initial stages are frequently extreme in character thus necessitating in the pioneers a degree of specialization that is found in relatively few species.

The most common of the primary areas are flood plains and islands forming in streams, and the steeper bluffs above stream banks. Associated with streams and bluffs are communities found only on rock surfaces but these may be found elsewhere as well. Finally, where erosion has progressed so that all the surface soil is removed, the denuded subsoil is exposed and pioneers in such habitats likewise initiate primary succession.

A. FLOOD PLAINS AND ISLANDS

The majority of the streams in the Piedmont are still actively cutting deeper into their beds but locally aggradation may be brought about, usually on a small scale. The resulting sand bars, islands, spits and narrow flood plains, when sufficiently developed, show a definite sequence of communities. Because they are small and frequently difficult of access, such areas often remain undisturbed for years and a fairly complete series of developmental stages was located by searching along many streams. Since the areas are invariably small and all are subject to radical disturbance by flooding, especially in their early stages, some irregularity in stand composition and rate of development is to be anticipated.

Tree species with their ages are presented for a series of primary habitats in Table 13. That the dominants and general trend are similar to mixed hardwood development on secondary bottomland habitats is apparent at once. This is as would be expected, for secondary succession is always a modification of the primary succession which was occurring in the habitat when the disturbance took place.

The earliest woody community is invariably a willow-alder thicket which may persist for a number of years. If the habitat remains poorly drained other hardwoods may not appear in significant numbers for a much longer time than on better-drained sites. That willow thrives in saturated or poorly drained soil from which other hardwoods may be excluded serves to explain why isolated willow clumps may occur in fairly mature bottomland hardwoods of secondary origin. The willows must be related to localized wet depressions where they

TABLE 13.—Ages of trees in a series of primary bottomland communities. REPR. indicates reproduction.

Station	Willow	Alder	Birch	Sycamore	Elm	Ash	Red Maple	Red Gum	Persimmon	Mulberry	Flowering Dogwood
52	10	+			REPR.	REPR.			REPR.		
51	5–15	+	REPR.	REPR.	REPR.	REPR.			REPR.		
50	10–20	+	3–12	2–10	REPR.	REPR.					
20	15–45				6–9	5–6					
16	46–48			12–15	?–16				REPR.		
17	48–50				8–12				REPR.		
18	40–55				30–32	10			REPR.		
19				35	28	8–16	10		REPR.		
22			20–55		19–20	10–32	13	REPR.	REPR.	10	
21					23–36	34–36	20–35	5–10		15	REPR.
14–15	50–52			45–55	27–60	50–55	25–42	38	20	30	REPR.

may become established at any time regardless of the vegetational development on the general floodplain which is elsewhere well drained. Thus the willow colonies are more nearly a primary development than a part of the secondary stand which surrounds them, for their time of appearance and their survival in competition are controlled by the local moist depressions within the better drained habitat.

In the primary communities listed, willow has a rather wide range of ages. New seedlings and sprouts continue to appear as long as moisture conditions are favorable. Again, the relative age of willow and the other hardwoods varies because the time when other hardwoods appear and their rate of increase depend largely upon the rate of change in drainage of the site.

Apparently birch and sycamore may or may not be members of the hardwood community following willow and, even where present, they do not represent a distinct stage of development. Elm, ash and red maple come in on primary sites much earlier in succession than on secondary sites. Red gum is not a part of the younger communities but it appears after elm-ash-maple dominance is established and then is usually an associated understory tree. Red mulberry is in much the same category. Dogwood is not important in the younger stands, in fact it is only in the older stands that its reproduction is noticeable. Persimmon reproduction may be found in stands of almost every age but trees are usually observed only in the oldest stands.

TABLE 14.—Occurrences of species of shrubs and vines in a series of primary bottomland communities of increasing age. Stands indicated by station numbers the same as in table 13.

Station	52	51	50	20	16	17	18	19	22	21	14
Cephalanthus occidentalis	×	×	×	×	×	×		×			
Sambucus canadensis	×	×	×	×	×	×	×	×	×		×
Viburnum nudum		×									
Ilex decidua			×		×	×		×		×	
Rubus spp.				×			×		×		×
Lonicera japonica				×	×	×	×		×	×	×
Rosa palustris					×	×	×	×	×		
Vitis rotundifolia							×	×		×	×
Smilax rotundifolia							×				
Evonymus americanus									×		×
Viburnum affine var. *hypomalacum*									×	×	×
Rhus toxicodendron var. *radicans*									×	×	×
Parthenocissus quinquefolia										×	×
Viburnum prunifolium											×
Tecuma radicans											
Tecoma radicans											×

The shrubs and vines of primary bottomland habitats (Table 14) are again much as in the secondary stands although they do not appear until the dominants have reached some maturity. The constant occurrence of buttonbush and elderberry is noteworthy. Their tabulated occurrences indicate that buttonbush tends to disappear as the stand closes up but that elderberry may remain a typical shrub in all stands. Deciduous holly is a characteristic species in the understory, sometimes assuming tree size. The vines, here as elsewhere in

bottoms, are present in great numbers. Honeysuckle is especially prolific and its masses of growth often pull down and interfere with growth of younger trees and seedlings.

The list of herbs (Table 15) is surprisingly short. It is not intended to be complete but includes all those species which are abundantly present and noticeable without search. All are typical of moist sites and, except for those of station 51, a relatively open situation, the others can scarcely be found except in partial shade and moist to saturated soil.

TABLE 15.—Herbs recorded in a series of primary bottomland stands which are arranged in order of increasing age. Stations as in table 13.

Stations	52	51	50	20	16	17	18	19	22	21	14
Viola spp.	×			×	×	×	×	×	×		
Boehmeria cylindrica	×			×	×	×	×	×	×	×	×
Carex sp.		×									
Rhexia mariana		×									
Cassia chamaecrista		×									
Verbena urticaefolia		×									
Diodia virginiana		×									
Saururus cernuus				×			×	×			
Ambrosia trifida				×	×	×	×	×	×		
Impatiens biflora									×		
Verbesina occidentalis										×	×

Study of the recorded observations on reproduction yields no evidence of probable subsequent changes in even the oldest of these primary stands. Because of the similarity to secondary stands it may reasonably be assumed that bottomland oaks and hickories would eventually appear and finally rise to dominance. However, it is apparent that the primary stands of elm-ash-red maple maintain themselves for much longer periods than comparable secondary stands. This is, of course, in accord with the generalization usually recognized, that the rate of primary succession is relatively slower than secondary.

B. BLUFFS

Bluffs of varying height are common along streams throughout the Piedmont. As to physical nature, the ordinary situation is a steep to vertical cliff with a bevelled portion at the top and an accumulation of talus at the base. Since the nature of the rock varies, some cliffs are far more eroded than others. In a few instances weathering and erosion may have cut the bevel almost down to the talus and the result is a long even slope. Between this extreme and the vertical rock cliff all possible variations may be found. The amount of talus below any bluff varies with the nature of the rock and the effects of stream erosion. When a stream bed parallels the base of a cliff the debris may be removed almost as fast as gravity deposits it. When the rock is not particularly resistant, undercutting of the bluff by stream action results. This speeds weathering and sometimes results in the erosion of cave-like depressions in the face of the bluff. Associated with these depressions and especially at their margins there is invariably an assemblage of typical mosses. Some characteristic species are

Aulacomnium heterostichum,[7] *Bartramia pomiferis, Cirriphyllum boscii, Thuidium delicatulum* and *Hypnum imponens.*

Insufficient information is at hand for a complete discussion of bluff habitats and vegetation in the Piedmont. However, some rather broad statements may safely be made which are applicable to a wide area.

The striking differences in vegetation on north and south facing bluffs as well as the factors involved in producing them are well known. In this vicinity where droughts occur periodically, and then usually during periods of hot weather, moisture conditions on south facing bluffs approach a critical point quite frequently. Soil or no soil, the south facing bluff is one of the most xeric habitats in the Piedmont and this is reflected in the vegetation. Trees are commonly scrubby and rarely form closed stands. Pine is not uncommon but xerophytic hardwoods are usually more abundant. The commonest trees are *Quercus marilandica* and *Q. stellata* and red cedar is present here, as elsewhere, but usually thriving surprisingly well. The shrubs likewise are xerophytic with Ericaceae usually predominating. Several species of Vaccinium always may be found, usually low and dwarfed in appearance, while *Polycodium* spp. is less common. *Batodendron arboreum,* larger and more conspicuous, is almost always present. The open, usually rocky slopes support oak-hickory forest comparable, but of even poorer development, to that which occurs on uplands of inferior site quality.

Herbs are commonly of the weedy type. In addition to scattered grasses, especially Andropogon and several species of Panicum, legumes are common. *Desmodium* spp. and *Lespedeza* spp. may be found everywhere as well as *Galactia regularis, Stylosanthes biflora, Centrosema virginianum* and *Strophostyles umbellata.* Composites include *Coreopsis verticillata, Hieracium gronovii,* several species of Eupatorium and many goldenrods. Less common are *Asclepits verticillata* and *Passiflora incarnata.* Many other species of fields and roadsides may occur sporadically.

Where bare rock is exposed, conditions are most extreme and here certain especially adapted species may often be found. Narrow leaves and wiry structure permit the growth of *Cyperus filiculmis, Stenophyllus capillaris* and *Houstonia tenuifolia,* any of which may occur in crevices or sandy depressions. Less frequently, the succulents *Talinum teretifolium* and *Diamorpha cymosa* may be found on granitic rock and *Arenaria brevifolia* will often be associated with them. Rarely the succulent xerophyte, *Manfreda virginica* may be found with these species.

The dry rocky bluffs provide a special habitat for several ferns which are scarcely found elsewhere. These include *Cheilanthes tomentosa* and *C. lanosa,* both infrequent in the lower Piedmont and, rarely, *Asplenium montanum,* more common at higher altitudes. *Woodsia obtusa* is fairly common as is *Dryopteris marginalis.* The few limestone outcrops which occur in the upper Piedmont

[7] Nomenclature of mosses as in A. J. Grout. Moss Flora of North America, 1928-1940.

are usually in the form of such bluffs. On them, *Pellaea atropurpurea* is almost invariably present and *Asplenium resiliens* has been found at several stations (Oosting, 1941).

The north facing bluff provides an extreme contrast in vegetation. Undoubtedly this constitutes the most favorable habitat for plant growth, largely through temperature-moisture conditions. The dominant vegetation is, when undisturbed, of postclimax nature and associated vegetation includes many species found nowhere else in the region. In this vicinity several of these species approach the limits of their ranges, and some are definitely growing at widely disjunct stations.

The bevel at the top of the shaded bluff supports vegetation related to the surrounding upland. Because of its position, oak-hickory forest in some form is usually present. Differences from the upland hardwoods are so slight that details here seem unnecessary.

The talus slopes and lower portions of the cliffs support, in addition to floodplain species, a group of others which make this a very special community.

The oaks include *Quercus phellos, Q. prinus, Q. alba, Q. borealis* var. *maxima,* and the hickories also tend to include lowland species such as shagbark and bitternut. With these may be tulip poplar, sycamore and other species from the flood plains and almost invariably some beech *(Fagus grandifolia)* as well as hard maple *(Acer floridanum)*. Restricted entirely to the talus slopes and an occasional old floodplain which has escaped disturbance, this complex of dominants must be postclimax to the much more generally prevalent oak-hickory forest of the uplands. The complex develops and survives only because of the exceptional local conditions provided by floodplain and bluff. The higher the bluff the greater the protection it affords and consequently the better development of the community. Another factor, of course, is the age and stability of the talus. Only on gently sloping, long undisturbed talus is the community well developed.. An incidental point is the characteristic position of beech which, on younger talus slopes, is always concentrated along the upper edge of the talus forming an irregular line. Here the bluff provides the greatest protection in ameliorating temperature and atmospheric moisture conditions.

The lesser tree species may include any that are associated with postclimax hardwoods (Table 16) as well as those listed for any bottomland hardwood communities. Succession of the dominants is similar to secondary bottomland hardwood development for the talus is not a truly primary habitat.

Shrubs include a number of bottomland species such as *Ilex monticola* and *I. decidua*. Several species of Viburnum are common as well as *Styrax grandifolia, Hydrangea arborescens, Cornus florida* and varieties of *Aesculus neglecta. Callicarpa americana* occurs here too but it is infrequent in the western part of the area. *Magnolia tripetala* is restricted to such habitats in the Piedmont and the pawpaws *(Asimina parviflora* and *A. triloba)* are most commonly found here. Woody vines are the same as those listed for rich flood plains and need not be enumerated.

Needless to say these rich talus slopes form the most favorable herb habitats of the region. A complete listing of species would be impossible because of its length. In addition to the numerous species of rich flood plains there are many more found only here. Among the orchids which occur almost invariably are *Tipularia discolor* and *Goodyera pubescens*. Somewhat less common are *Orchis spectabilis, Liparis liliifolia* and *Aplectrum hyemale*. Occurring only locally, but then sometimes rather abundant, are the ladyslippers *(Cypripedium acaule, C. calceolus* var. *pubescens)*. Many other spring flowering species can be found only in these rich, protected habitats. Examples are *Chamaelirium luteum, Uvularia sessilifolia, U. perfoliata, Erythronium americanum, Smilacina racemosa, Polygonatum pubescens, Trillium catesbaei* and *Sanguinaria canadensis*. Wild ginger *(A. arifolium, A. virginicum)* occurs here as in other rich hardwoods but the uncommon *Asarum canadense* var. *reflexum*, when it is found, will only be on rich talus slopes. Several species of Ranunculus appear most often here while the related *Anemonella thalictroides, Hepatica americana, Anemone quinquefolia, Cimicifuga racemosa* and *Actaea alba*, which is rare, can scarcely be found elsewhere. The usually sandy flat at the base of the talus almost invariably supports *Zanthorhiza apiifolia* and *Podophyllum peltatum*. The rather rare Dicentras *(D. cucullaria, D. canadensis)* as well as the commoner *Corydalis flavula* are found in such habitats in the Piedmont. Early flowering species of Cardamine and Dentaria are always present. Others frequently found include *Aruncus sylvester*, and *Waldsteinia doniana*. *Pyrola americana* has been collected occasionally in the region. More common species are *Geranium maculatum, Osmorhiza claytoni, Zizia aurea* and *Amsonia tabernaemontana*.

Pteridophytes requiring shade and moisture are found mostly along the base of bluffs. *Botrychium virginianum* occurs regularly as do *Cystopteris fragilis, Dryopteris noveboracensis, D. intermedia, D. hexagonoptera* and *Athyrium asplenioides*. *Adiantum pedatum* and *Ophioglossum vulgatum* are not common and *Lygodium palmatum* is rare, but all are associated with rich talus slopes or the shaded flood plain below.

Not infrequently a bend in a stream will have cut back into a bluff to form a cove-like area whose widest opening faces north. Here the ordinary effects of north-facing bluffs are intensified and the results are apparent in the vegetation which is richer than anywhere else. Here may be found the rare species widely disjunct from their normal ranges and those species whose special requirements permit them to grow only in the habitat provided by the shelter of the bluff.

The most striking example of this disjunct range is the small hemlock community on Swift Creek, south of Cary. Here the bluff is high and curving and, in its protection, is a small stand of *Tsuga canadensis*. The trees were at one time more numerous according to local residents but a few have been cut and some have died. Reproduction is not abundant but seems adequate for maintenance of the stand. However, visitors have removed seedlings and small trees for a number of years so that it now appears the stand may not be permanent.

Another example is the white pine stand at the confluence of the Deep and Rocky Rivers in Lee County. This stand is of much greater extent than the hemlock but is restricted to the north facing bluff along the river.

Both of these tree species are far from the limits of their normal range. Their nearest, natural abundant occurrence is in the foothills and mountains of western North Carolina. The same factors which permit the growth of these two trees in the lower Piedmont are operating to some extent on every north facing bluff. As a result, several of the species previously listed for talus slopes are much more common to the west in the mountains and northward. This is, of course, excellent supporting evidence for designating the usual hardwood community of protected talus and flood plain as postclimax.

The bluff proper, or cliff portion of the bluff, may not be a particularly favorable plant habitat if steep and high. However, certain species somewhat beyond their most favorable range may be found growing here in the Piedmont. Conditions are apparently such that these species can compete with those of the Piedmont and even exclude many of them. The resulting vegetation on the upper margins of the talus and on the most favorable slopes of the bluffs is much more characteristically montane than Piedmont in nature. Thickets of *Kalmia latifolia* are common and in the most favorable sites *Rhododendron catawbiense* is an associate. Other shrubs, not previously mentioned and commonly found on the cliffs and bevel are *Calycanthus fertilis, Benzoin aestivale, Symplocos tinctoria* and *Chionanthus virginica. Leucothoe racemosa* occurs infrequently as does *Staphylea trifoliata.*

Further contributing to the montane aspect are herbs such as *Galax aphylla* and *Gaultheria procumbens.* Occasionally *Dicentra eximia* occurs on a rocky shelf and *Heuchera americana* is common in the crevices of these shaded cliffs. Needless to say, when montane or northern species occur in the Piedmont they will be found associated with north facing bluffs. Among these are several pteridophytes, not yet mentioned, which may be found on shaded rocks. The two polypody ferns *(P. polypodioides, P. virginianum)* may form solid mats here, and more locally *Camptosorus rhizophyllus* may also be found, as well as *Asplenium trichomanes* and the several ferns listed for talus slopes. In these same habitats *Sedum ternatum* may also form dense mats on moist shaded rocks and *Epigaea repens* and *Mitchella repens* are almost invariably present.

These species indicate something of the richness of the flora associated with north facing bluffs. Without these habitats the Piedmont flora would be much reduced and, for the taxonomist, they provide constant surprises and extensions of distribution records. The plant geographers too must know these places and the ecologist must study them to contribute to the interpretation of the special reaction of species as they approach the limits of their ranges.

C. EROSION

It is generally recognized that the soils of the Piedmont have long been subjected to erosion, especially sheet erosion, and that even the best of upland soils have lost a part of the A horizon. Locally there are areas from which

sheet erosion has removed all of the A horizon and, in some instances, the erosion may have progressed to the gullying stage. Much of the serious erosion has now been checked through drastic control methods where gullying has begun, and simply by planting fields subject to sheet erosion.

When fields subject only to sheet erosion are abandoned the development of natural vegetation is usually sufficient to bring the erosion to a stop in a few years. While still in the herb stages of revegetation the areas of most serious erosion will be marked by a thin covering of vegetation, largely *Aristida dichotoma, Plantago aristata,* and *Diodia teres,* which from a distance appear as bald spots surrounded by the typical old field herbs. Eventually these spots may support the Andropogon stages of succession and finally pine but the rate of change will be reduced. It should be noted that, on eroded fields, the normal stages and completeness of herb cover may be absent. However, as also stated by McQuilkin (1940), it is possible for pine to occupy such sites even though the usual herb stages have never developed. It should be emphasized that the direct invasion of eroded fields by pine is not to be expected except under special conditions. When a good seed year happens to coincide with exceptionally favorable moisture conditions throughout the period of seedling development, pine may become established. The quality of the resulting stand is never comparable to that of one on a good site.

Other things being equal, the site quality varies inversely with the degree of erosion. The poorer the site the fewer herbs there are which can survive there. When herb competition is reduced on poor soils lichens thrive and the presence of Cladoniae[8] may be taken as an indicator of poor site which here usually is the result of erosion. The greater the ground cover of lichens the poorer the site and the lower the site index. The same may be said for certain mosses but they are not as conspicuous and apparently not as responsive. The stands with the greatest ground cover of Cladonia are unevenly stocked, and the trees may have made such uneven growth that they appear to be of all ages when in reality they are not.

If a good seed year is followed by exceptionally favorable growing conditions an occasional well-stocked stand may develop on eroded soil. Such stands do not have this ragged appearance and at middle age may superficially appear quite normal. However when the age of the stand is determined it will be found that although growth was uniform throughout the stand, it was relatively

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8 Fairly representative collections of Cladonia from Duke Forest and vicinity are deposited in the Duke Herbarium. All have been identified or checked by Alexander W. Evans. Habitat data on these specimens indicate that any of the following may be expected in sites similar to the ones under discussion. Species on this list have been repeatedly collected. There are others which occur less frequently.

C. subcariosa Nyl.
C. apodocarpa Robbins
C. piedmontensis Merrill
C. verticillata (Hoffm.) Schaer.
C. tenuis (Floerke) Harm.
C. cristatella Tuck.
C. calycantha Del.
C. strepsilis (Ach.) Vainio
C. papillaria (Ehrh.) Hoffm.
C. mitrula f. *imbricatula* (Nyl.) Vainio

slow. It appears now that such stands may be recognized by the slow ecological maturation which is indicated by the absence of or the poor development of hardwood understory and shrubs. In addition, the herb layer is characterized by an abundance of legumes, especially Lespedeza and Desmodium species. Similar ecological retardation may be produced by extreme overstocking on good sites but it seems particularly pronounced when heavy stocking occurs on eroded soil.

The natural revegetation of a gullyed area is a long process which, if erosion is active, may not be complete for an indefinite period. The constant exposure of new subsoil at the head of a gully permits little or no opportunity for plants to establish themselves there. Until this head erosion is checked the gullying usually continues. However vegetation is not completely absent. Cladoniae are usually present in quantity, especially in those small areas where enough pine needles have accumulated to partically check erosion. On the outwashed fans near the gully mouth, and on the sidewalls and isolated terraces a considerable number of herbs may be found. These include almost all species of old fields and the degree of stability will determine how nearly the herbaceous cover approaches the mature or Andropogon stage. The legumes of old fields are particularly numerous and are augmented by several more legumes characteristic of roadsides, and waste places.

D. BARE ROCK

Of very minor importance as a plant habitat but occurring sporadically throughout the Piedmont are boulders and, less commonly, rock outcrops. Locally boulders may be numerous but never large, and rock outcrops are commonly not extensive. Although the species of lichens, mosses and liverworts occupying rock habitats appear with some degree of regularity, still almost every rock must be considered as a special habitat if associations or successional trends are described. The nature of the rock, the number of crevices, the degree of exposure to sun or shade, moisture relations and many other factors contribute to make generalizations inadvisable.

Some general information on mosses to be expected on boulders and isolated rocks is given by Anderson (1938) in his introduction to "The Mosses of North Carolina" and greater detail is given for individual species in later papers of this same series. Detailed studies have been made of the development of vegetation upon the localized extensive rock outcrops near the fall-line as well as in the mountains of the state (Oosting and Anderson, 1937, 1939). These papers give the specialist interested in lichens and bryophytes some idea of the nature of Piedmont rock communities. The vegetation on boulders and small outcrops is present in the form of isolated "micro-communities" which are not necessarily determined by the dominant vegetation. Such rock communities contribute little or nothing to the major successional trends. In view of the specialized nature of rock communities both taxonomically and ecologically, further discussion would appear to be out of place.

III. Climax Communities

A. CLIMAX

The past history of the Piedmont precludes the possibility of virgin forest remaining in the area. Today mature hardwood stands which are even relatively free from disturbance are uncommon and always of limited extent. The earliest white settlers appeared in what is now Durham County about the middle of the eighteenth century (Boyd, 1925). Therefore when occasional hardwood stands are found which include trees 200-300 years of age and which show little evidence of recent disturbance, they must be accepted as samples of the extensive hardwood forests which preceded the white man.

Such stands can be found but, almost invariably, they occupy sites which for some reason could not be cultivated to the best advantage. Usually they are associated with topographic irregularities and sometimes with inferior site quality. These things must therefore be considered when interpreting the ecological significance of the hardwood stands. Without exception the major components of the dominant strata are oaks and hickories. The species and their proportionate numbers may vary from stand to stand but certain "binding species" are consistently present both in the dominant and dependent strata. The oak-hickory dominated community is widespread in the Piedmont. Local conditions, often edaphic, result in variation or "segregation" to form different combinations of the dominants. The similarities of these communities, however, in their mode of origin, composition and growth-form bind them into one complex, abstract type—oak-hickory.

Obviously a complex which is so widespread and occurs so consistently must be climatically controlled and its variations must be determined by specific local conditions. Add to this reasoning the fact that all successional trends lead to final oak-hickory dominance which maintains itself indefinitely if left undisturbed, and oak-hickory must be recognized as the climax type for the vicinity.

Two extremes in local variation must be given special attention for their characteristics would hardly fit all the criteria and generalizations applied to the climax in the above discussion. Bottomlands and rich, shaded talus slopes support a successional trend quite distinct from that of uplands but nevertheless one which leads toward oak-hickory. However, the species making up the final stabilized community are quite different from those of the climatic climax. Oaks and hickories never found in the upland hardwoods occur here, and, associated or sharing dominance with them, are several other mesophytic hardwoods whose range is northward and westward where they are a part of the climax. In the Piedmont these communities are obviously *postclimax* (Clements, 1936). The opposite extreme produced by local conditions is xerophytic. The dominants are perhaps more closely related to the climax in that they appear sporadically in climax communities. However, when xerarch succession finally terminates in a stable community these xerophytic species (oaks especially) are the dominants and the stand is open and scrubby. This segregate of oak-hickory climax may occur in more than one type of habitat. It appears

on dry south facing bluffs, on thin soil about rock outcrops, and, here most commonly, on Iredell and Orange soils which characteristically have an extremely impervious clay stratum only a few inches below the surface. Having its own successional development, controlled by edaphic factors, stable, and maintaining itself indefinitely the community is distinct and may be termed *preclimax*.

In addition to these extremes of mesophytism the foresters (Korstian and Maughan, 1935) recognize several forest types among the upland hardwoods. In characterizing these types they suggest the probability of the successional nature of those in which pine occupies an important position. It is obvious from the preceding discussion of pine communities that this can be the only interpretation and that all such forest types must be recognized as transitional between pine and hardwood dominance

Three hardwood forest-types are recognized on the uplands, namely: the white oak-black oak-red oak type, the white oak-post oak type, and the white oak type. The last named type, is mapped as occupying only a half of one percent of all the upland hardwood on the Duke Forest, and is elsewhere equally rare and local. Ecologically it can be no more than a minor local variation temporarily dominanted by white oak alone. The other two types are, however, fairly distinct and usually recognizable without difficulty. That they bear a successional relationship to each other, as Korstian and Maughan suggest, is possible but not probable in terms of the ecological evidence available. It seems more reasonable to recognize the two forest types as variants of the oak-hickory climax which are determined by site. Both types are made up of trees of uneven age, usually include individuals which are overmature, and the reproduction indicates the probability of indefinite continuation of the *status quo*. The limited occurrence of the white oak-post oak type and its association with inferior exposure, drier ridges and knolls, and apparently poorer soils all add to the conclusion that the type is a variation of the climax maintained by those sites which will remain indefinitely somewhat more xeric than the general terrain.

The maps of forest types on the Duke Forest show that the acreage of the white oak-black oak-red oak type exceeds the white oak-post oak in a proportion of about thirteen to one. (The two types are hereafter termed white oak and post oak types respectively). This proportion includes, for both types, young stands, areas now poorly stocked because of selective cutting or disturbance, and acreages so small as to be out of consideration ecologically. However, the relative importance of the two seems fairly indicated. Because of these irregularities only an occasional stand could be used in a statistical approach to the composition and structure of the climax. Mature stands of sufficient extent to permit adequate sampling are infrequent and such larger areas which show no recent effects of some form of disturbance are rare.

Three complete series of quadrat data were obtained for each of the two climax oak-hickory types. All stands were large enough to permit sampling without approaching the transitions to contiguous stands and all were relatively free

from disturbance of any kind. The characteristic rolling topography of the uplands was typical of these areas and so it is assumed that minor variations in slope and exposure are equally weighted for all stands. The larger overstory trees were invariably uneven aged (Fig. 17), usually two hundred years old and older, and some individuals as old as three hundred years.

The abundance and distribution of all individuals of tree species in the stands sampled are shown by frequency and density values in Tables 16 and 17. Judging by these counts it is apparent that the two types are closely related yet with distinctive dissimilarities.

Overstory species.—In general all overstory species are found in every size-class of some stand of both types. *Quercus velutina* is not recorded for the overstory of the post oak type, however, and even in the understory its frequency and density are consistently low. Comparing its values in post oak with those in white oak it becomes more strongly apparent why it should be classed with the white oak as a character species for a forest type.

Both white and post oak appear in every size class in every stand. However, this apparent similarity obscures the real differences in composition, for numbers and distribution of the two species in the two types are very unlike. *Quercus alba* exceeds *Q. stellata* in numbers and frequency in all size classes of both types except the overstory of the post oak type. This must indicate survival and maturation of a greater percentage of post oak seedlings under the conditions obtaining on post oak sites. Density and frequency of *Q. alba* are about two or three times greater in the white oak types than the post oak types. This seems fairly distinctive but the same values for *Q. stellata* show it to be three to ten times denser in the post oak than the white oak types and to have even a greater frequency differential. It would appear that the numbers and distribution of the two species might safely be taken as indicators of type. Judging from these data, the density and frequency of *Q. alba* are about ten times greater than those of *Q. stellata* in the reproductive size classes of the white oak type and the proportions slightly less in the tree sizes. In the post oak type the density and frequency for the two species are very nearly the same in all size classes except the overstory where *Q. stellata* has double the values of *Q. alba* in both density and frequency.

Other species of oak do not exhibit such marked differences for the two types. All have lower frequencies and densities regardless of the type and this makes differences less obvious. All may appear in any size class of either type. The data indicate a somewhat greater irregularity for the post oak type in that other species of oak occur not at all, in relatively large numbers, or as isolated individuals. Undoubtedly the white oak sites are, as a whole, more favorable to black, southern red, northern red and scarlet oaks. *Q. marilandica* is however, definitely related to the post oak type. Characteristically a scrubby tree, it typically maintains dominance only on the poorest sites. In the post oak climax type it is usually present with a low frequency and density in all size classes except the overstory. Rarely does it exceed the understory status. When

TABLE 16.—Density and frequency of trees in over and understory of all upland oak-hickory series.

Size Class	Under story						Over story					
Type	White Oak			Post Oak			White Oak			Post Oak		
Series	15	16	17	18	19	20	15	16	17	18	19	20
Quercus alba	1.0	0.4	0.6	0.6	1.3	1.5	1.4	1.2	1.0	0.1	0.7	1.0
	40	60	20	60	70	80	70	80	50	10	60	70
Carya spp.	2.8	5.2	1.6	1.1	2.9	2.1	0.1	1.2	1.3	0.3	0.3	0.1
	80	70	70	50	70	60	10	60	60	30	30	10
Quercus velutina	0.4	0.5	0.2	0.1	0.1	0.1	0.3	0.1				
	20	30	10	10	10	10	30	10				
Q. stellata	0.1			0.4	1.4	1.2	0.3	0.1	0.3	1.3	1.6	0.9
	10			40	80	50	10	10	30	80	80	50
Q. borealis var. *maxima*		0.3		0.1				0.1		0.2		
		20		10				10		10		
Q. rubra	0.2	0.1				0.3		0.1	0.1	0.3		0.3
	20	10				30		10	10	30		30
Q. coccinea		0.2		0.6			0.2		0.1	0.2		0.1
		20		40			20		10	20		10
Pinus taeda	0.2	0.6		0.1			0.1					
	30	20		10			10					
Oxydendrum arboreum	6.1	1.4	4.3	0.2	0.1	2.8						
	50	100	100	20	10	60						
Cornus florida	5.0	3.9	6.3	7.9	1.1	1.7						
	70	90	100	100	50	90						
Nyssa sylvatica	1.4	0.3	1.3	0.3	0.7	1.3			0.1			
	20	60	90	20	50	50			10			
Acer rubrum	0.9	0.4	1.3	4.4		0.1						
	30	60	50	100		10						
Juniperus virginiana	0.3	0.9		1.6	2.0	0.5						
	70	30		80	80	50						

TABLE 16.—(Continued)

Size Class	Under story						Over story					
Type	White Oak			Post Oak			White Oak			Post Oak		
Series	15	16	17	18	19	20	15	16	17	18	19	20
Diospyros virginiana		0.1		0.1				0.1				
		10		10				10				
Liriodendron tulipifera	0.1					0.1						
	10					10						
Amelanchier canadensis	0.1											
	10											
Liquidambar styraciflua		0.1		1.2	0.1							
		10		50	10							
Prunus serotina		0.2										
		10										
Ilex decidua		0.2										
		10										
Morus rubra		0.2										
		10										
Pinus echinata				0.8	0.9	1.4				0.1		0.8
				30	50	70				10		50
Quercus marilandica				0.1	0.6	0.7						0.1
				10	30	50						10
Fraxinus americana				0.7	0.4	0.1						
				60	20	10						
Ulmus spp.					0.4							
					30							
Cercis canadensis				0.1								
				10								
Chionanthus virginica				0.1								
				10								

present in association with the better oaks it may be taken as an indicator of the post oak type.

It is regrettable that the data for the several species of hickory could not have been kept separately for, as with the oaks there are undoubtedly some species-type relationships. The species which are relatively common and are probably included in these counts are *Carya carolinae-septentrionalis*, *C. alba*, and *C. glabra*. To a lesser extent *C. pallida* and *C. microcarpa* are also probabilities. Taken collectively the density and frequency of hickory in the white oak type slightly exceed those values for the post oak type in all size classes. The differential increases from seedling to crown cover but is negligible in the lesser size classes. In the overstory of the white oak type hickory density is almost four times that of the post oak type and frequency is about double. Considering that in these same stands hickory density and frequency are about the same in understory and lesser sizes it appears that the total of hickories in the white oak type considerably exceeds that of the post oak type and that in the latter type hickory is a much less important dominant.

The data for the occurrence of pine seem particularly significant. In the stands studied, short leaf pine was restricted to the post oak type and loblolly pine to the white oak type with the exception of a single tree in the understory of one post oak stand. This is not always true but it frequently is. As previously indicated, loblolly tends to occupy better sites than shortleaf when in pure stands. Obviously the generalization is applicable to the distribution of the pines in these segregates of the climax. It should be emphasized that the presence of pine in the climax community is probably a normal condition. In fact, the pines probably occurred in much the same manner in the virgin hardwood forests of the Piedmont. Where catastrophic events may occasionally have swept a forest area clear of trees there may have resulted pure stands of loblolly or shortleaf pine which were again replaced by hardwoods in the normal course of succession. However, within the extensive undisturbed hardwood areas there must have been pines with low densities and frequencies in all size classes. These could not reproduce under the hardwoods but as is true today the death of an overstory individual permitted germination and growth of a number of pines in the resulting opening. Some few of these must have grown to maturity and have furnished seed sources for other generations of pine when local conditions again became favorable.

Understory Species.—There is first a group of species common to both types. These include *Oxydendrum arboreum*, *Cornus florida*, *Nyssa sylvatica*, *Acer rubrum*, *Juniperus virginiana* and *Diospyros virginiana*. The first four may be taken as the character species in the understory of the upland hardwood forest. Rarely do any of them attain the dominant stratum yet they are in no sense dependent upon the dominant stratum for survival.

The species of the understory consistently have a higher density and frequency in all size classes of the white oak than the post oak type. This can well be

attributed to the relative quality of the sites. All the species except sourwood reproduce freely and have high densities in the younger size classes. In the transgressive sizes there is a high mortality but a high frequency is maintained. Sourwood seems to produce fewer seedlings but survival is obviously better, for its numbers increase in the larger size classes. Persimmon is an infrequent member of the understory although consistently present in lesser size classes with a low frequency.

Tulip poplar and red gum are scarcely recognizable as typical members of the upland hardwood forest for they appear sporadically and in small numbers. The frequency-density values fairly well indicate their importance.

Of the remaining species, *Amelanchier canadensis, Sassafras officinale, Prunus serotina, Ilex decidua* appear only in the white oak type and ash, elm, ironwood and redbud only in the post oak type. Perhaps not too much significance should be attached to this distribution. Further study might well change the picture. None of these species are important in upland hardwoods. In fact, deciduous holly, red mulberry and ironwood are typically lowland subordinate species.

Basal Area.—The basal areas of trees one inch d.b.h and larger are given in Table 18 for all series of climax hardwoods. These data strengthen the conclusions drawn from density-frequency values in many respects and support the contention that two expressions of the climax are represented in the six series of quadrats.

In the stands of the white oak type, *Q. alba* made up 52% of the total basal area and *Q. stellata* only 8.5%, whereas in the post oak type the values were 19.7% and 33.9% respectively. The total basal area on the white oak sites exceeded that of post oak sites by 26.9% and this must be an indication of the superior site quality. This larger value is related both to size of dominants and numbers of lesser individuals. Oak and hickory accounted for 86.9% of the total basal area of white oak stands but only 78.8% of post oak stands. This difference again is related to site quality. Post oak stands are more open than white oak and therefore permit growth and survival of relatively more pine. The latter contributes 12.3% of the basal area in post oak and only 1.9% in white oak types. Another important difference in distribution of basal area occurs in the characteristic understory species, sourwood and dogwood. These comprise 8.4% of the total in white oak and only 4.6% in post oak for they have a lower density. Sourwood has twice the basal area of dogwood in the white oak stands but dogwood has three times that of sourwood in the post oak type.

Phytographs.—The differences in the relationships of the dominants of the two types are emphasized by the phytographs shown in Figure 16. Percent of total density, frequency, basal area and size classes are here graphically shown (data in Table 19) for each of the major species of the overstory and as they occur in each type.

TABLE 17.—Density and frequency of trees in transgressive and seedling sizes for all upland oak–hickory series.

Size class	Under one foot						Over one foot					
Type	White Oak			Post Oak			White Oak			Post Oak		
Series	15	16	17	18	19	20	15	16	17	18	19	20
Quercus alba	103.1	268.8	138.1	5.6	18.1	40.0	15.6	23.1	16.3	3.1	8.8	3.1
	100	100	100	40	90	100	50	90	60	40	40	20
Carya spp.	36.3	45.6	80.6	58.1	23.8	17.5	14.4	19.4	27.5	25.0	26.9	14.4
	100	100	100	100	90	100	90	90	100	90	100	90
Quercus velutina	5.6	12.5	12.5	5.6	9.4	3.8	7.5	6.9	11.9	2.5	5.0	3.8
	50	60	80	60	70	40	40	40	80	30	30	50
Q. stellata			2.5	42.5	18.1	30.0		0.6	0.6	0.6	3.8	7.5
			20	100	60	70		10	10	10	20	40
Q. borealis var. *maxima*	1.9	2.5	1.9	11.3		1.3	1.9	1.3		9.4		
	20	20	30	80		10	20	20		40		
Q. rubra	0.6	1.9	3.8	6.3		3.1	0.6		0.6		0.6	0.6
	10	20	50	50		20	10		10		10	10
Q. coccinea	1.9	18.1	5.0	13.1	0.6	2.5	2.5	3.8	12.5	23.8		1.9
	20	80	40	70	10	40	10	30	60	90		20
Pinus taeda	3.8	1.9	0.6				0.6	0.6				
	20	30	10				10	10				
Oxydendrum arboreum	1.9	0.6	1.9			0.6	2.5	6.9	7.5			5.6
	30	10	30			10	30	60	70			20
Cornus florida	86.3	63.1	80.6	27.5	5.6	9.4	38.8	12.5	29.4	21.3	6.3	5.6
	100	100	90	90	20	30	100	100	90	90	20	30
Nyssa sylvatica	0.6	15.6	8.8	1.3	0.6	5.0	4.4	21.8	16.9	5.0	1.3	9.4
	10	70	80	20	10	30	90	90	90	20	20	70
Acer rubrum	51.3	41.3	8.8	78.8	1.9	1.3	8.8	8.1	15.6	28.1	2.5	0.6
	80	100	70	100	20	20	50	60	80	90	10	10
Juniperus virginiana	1.3	1.9		1.3	4.4	1.3	3.8	0.6		4.4	5.0	1.9
	20	30		20	60	20	40	10		20	50	20

TABLE 17.—(Continued)

Size class	Under one foot						Over one foot					
Type	White Oak			Post Oak			White Oak			Post Oak		
Series	15	16	17	18	19	20	15	16	17	18	19	20
Diospyros virginiana	8.1	1.9	0.6	0.6		0.6	5.0	1.3	0.6	1.3	0.6	0.6
	50	20	10	10		10	50	20	10	10	10	10
Amelanchier canadensis		1.8	0.6				0.6	1.3				
		30	10				10	10				
Sassafras officinale	3.8	8.1	3.1					3.8	0.6			
	20	80	40					50	10			
Liquidambar styraciflua	0.6	0.6								0.6		
	10	10								10		
Prunus serotina							1.9	0.6			1.3	
							20	10			10	
Morus rubra							1.3			0.6		
							20			10		
Pinus echinata					3.8	8.1					3.8	5.6
					50	50					30	30
Quercus marilandica					10.6	4.4					5.6	5.6
					60	30					60	30
Fraxinus americana					1.3	0.6				1.9	2.5	
					10	10				20	40	
Ulmus spp.				0.6	2.5	1.3					0.6	0.6
				10	20	20					10	10
Carpinus caroliniana				0.6						1.3		
				10						20		

TABLE 18.—Basal area of tree species in three series each of white oak and post oak types of upland climax hardwoods.

Series	White Oak Type								Post Oak Type							
	15		16		17		Total		18		19		20		Total	
	SQ. FT.	%	SQ. FT.	%	SQ. FT.	%	SQ. FT.	%	SQ. FT.	%	SQ. FT.	%	SQ. FT.	%	SQ. FT.	%
Quercus alba	23.44	55.2	29.98	63.4	14.06	35.3	67.48	52.1	2.00	4.8	9.60	32.8	8.53	26.4	20.13	19.7
Q. stellata	4.09	9.6	1.89	4.0	5.08	12.7	11.06	8.5	13.39	32.5	15.18	51.9	6.00	18.9	34.57	33.9
Carya spp.	1.85	4.3	6.12	12.9	8.56	21.5	16.53	12.8	5.79	14.0	1.98	6.7	1.01	3.1	8.78	8.6
Quercus coccinea	4.04	9.5	0.01	0.02	2.18	5.4	6.23	4.8	5.21	12.6			1.26	3.9	6.47	6.3
Q. rubra	0.22	0.5	0.36	0.7	3.14	7.8	3.72	2.9	4.09	9.9			1.47	4.6	5.56	5.5
Q. velutina	1.59	3.7	5.31	11.2	0.01	0.02	6.91	5.3	0.01	0.02	0.02	0.06	0.17	0.5	0.2	0.2
Q. borealis var. *maxima*			0.62	1.3			0.62	0.5	2.76	6.6					2.76	2.7
Oxydendrum arboreum	3.56	8.3	0.97	2.0	2.7	6.7	7.23	5.6	0.11	0.2	0.35	1.1	0.64	2.0	1.10	1.1
Cornus florida	0.85	2.0	0.64	1.3	2.17	5.4	3.66	2.8	3.09	7.5	0.14	0.4	0.38	1.2	3.61	3.5
Nyssa sylvatica	0.66	1.5	0.09	0.1	1.8	4.5	2.55	2.0	0.05	0.1	0.08	0.2	0.93	2.9	1.06	1.0
Acer rubrum	0.06	0.1	0.12	0.2	0.09	0.2	0.27	0.2	1.14	2.7			0.02	0.06	1.16	1.1
Juniperus virginiana	1.06	0.1	0.23	0.4			0.29	0.2	0.44	1.0	0.9	3.0	0.1	0.3	1.44	1.4
Pinus taeda	1.65	3.8	0.26	0.5			1.91	1.5	0.14	0.3					0.14	0.14
Liquidambar styraciflua			0.08	0.1			0.08	0.06	0.35	0.8	0.09	0.3			0.44	0.43
Diospyros virginiana			0.43	0.9			0.43	0.3	0.02	0.04					0.02	0.02
Liriodendron tulipifera	0.35	0.8					0.35	0.3					0.35	1.1	0.35	0.34
Amelanchier canadensis	0.01	0.02					0.01	0.01								
Morus rubra			0.10	0.2			0.10	0.07								
Prunus serotina			0.03	0.06			0.03	0.02								
Ilex decidua			0.01	0.02			0.01	0.01								
Pinus echinata									2.45	5.9	0.37	1.2	9.29	29.4	12.11	11.9
Quercus marilandica									0.02	0.04	0.42	1.4	1.41	4.4	1.85	1.8
Fraxinus americana									0.1	0.2	0.06	0.2	0.02	0.06	0.18	0.18
Ulmus alata											0.05	0.1			0.05	0.05
Cercis canadensis									0.02	0.04					0.02	0.02
Chionanthus viriginica									0.01	0.02					0.01	0.01

TABLE 19.—Data upon which phytographs in Fig. 16 are based. Percent of total density, and basal area, per cent of four size classes and frequency distribution for the overstory species of the white oak (W) and the post oak (P) climax types.

	Density		Frequency		Size classes		Basal area	
	W	P	W	P	W	P	W	P
Quercus alba	43.9	21.4	66.6	36.6	100	100	61.6	22.6
Quercus stellata	8.5	45.2	16.6	23.3	100	100	10.1	40.1
Carya spp.	31.7	8.3	43.3	23.3	100	100	10.8	5.2
Quercus coccinea	3.6	3.5	10.0	10.0	100	100	5.7	7.9
Q. rubra	2.4	7.1	6.6	16.6	100	100	2.8	6.9
Q. velutina	4.8		13.3		100		9.5	
Q. borealis var. *maxima*	1.2	2.3	3.3	3.3	100	100	0.4	2.6
Q. marilandica		1.1		3.3		100		1.0
Pinus spp.	1.2	10.7	3.3	20.0	100	100	0.7	13.3

The contrast in relative importance of white and post oaks is immediately recognizable and is obviously one of the major differences among the dominants. Of the species shown, all are present in each of four size classes indicating their permanency in the types. However, no black oak appeared in the overstory of the post oak type and no black jack oak was found in the white oak type. Black gum and persimmon also appeared in the overstory of the white oak type but in very small numbers.

In the white oak type the values for *Q. alba, Q. velutina* and *Carya* spp. exceed those for the post oak type in every respect. The high percentage values of these three species result in lowered values for the other species in the same stands. As a result, the comparative values for other species are all greater to some extent for the post oak types. These diagrams further emphasize the indicator significance of a preponderance of *Q. stellata*, especially when *Q. marilandica* is present and when *Q. rubra* and *Pinus echinata* seem fairly numerous and widespread.

Shrubs and Vines.—The numbers of shrubs and vines are low as to species and individuals and only a few of the species are consistently present or evenly distributed. Differences in numbers of seedlings and individuals more than one foot tall did not appear to be significant enough to publish the counts separately. Accordingly the density and frequency values in Table 20 represent all individuals of any size. In passing it may be worth recording that the numbers of individuals in the mature size class (over 1 foot tall) are markedly less than the numbers of seedlings in every instance but the frequencies are not much less.

The data indicate only two really common shrubs, *Viburnum affine* var. *hypomalacum* and *Polycodium* spp. (*P. neglectum* most common). These two are outstanding above all others because of their relatively high frequencies and densities. Individuals of *Viburnum prunifolium* and *Chionanthus virginica* appear constantly enough to make this pair of species distinctive in frequency and density but to a lesser extent than the first two named.

Amelanchier canadensis, Ilex opaca and *Viburnum acerifolium* occur only in the white oak stands and *Azalea nudiflora* and *Viburnum rufidulum* are

recorded only in the post oak type. What degree of significance may be attached to this distribution is doubtful. It is possible that these species may be used as site indicators, for *Ilex opaca* and *V. acerifolium* are certainly infrequent anywhere but on the better sites. On the other hand *V. rufidulum* and Azalea are not properly described as species of poor sites. The data suggest that *Rosa virginiana* is favored by the post oak environment but evidence is lacking. Like styrax, hawthorn, strawberry bush and blueberries, it is more apt to appear sporadically and with no apparent reason. The low frequencies and

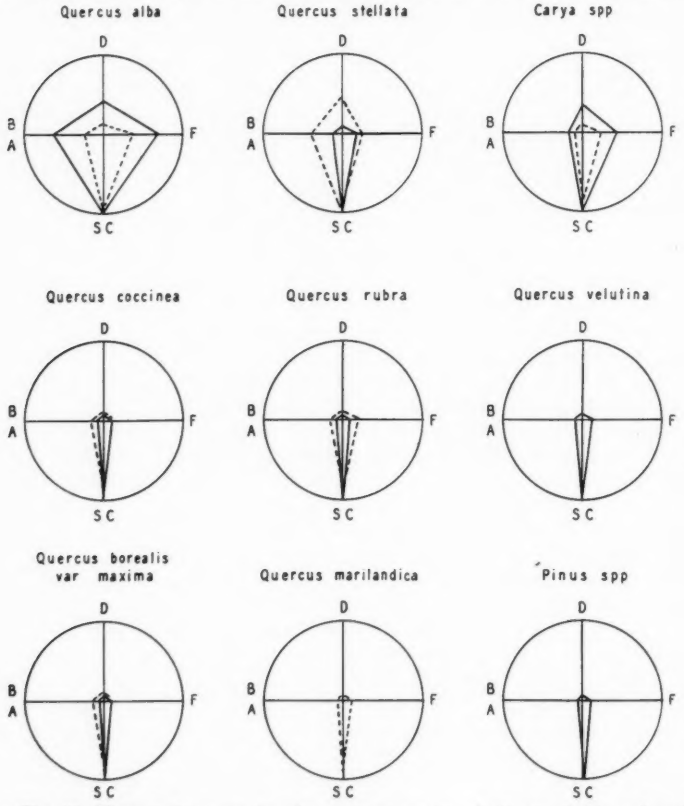

Fig. 16. Phytographs comparing the overstory species of the two (white oak and post oak) climax types. Values for the white oak type are indicated by solid lines, for the post oak type by broken lines. D—percent of total tree density, F—frequency percent, SC—percent of four size classes (overstory, understory, transgressives, seedlings) in which the species was found. Zero is the center, 100 percent the periphery of the circle.

TABLE 20.—Density and frequency of shrubs and vines in climax oak-hickory stands.

	White Oak Series				Post Oak Series			
Series	15	16	17	Aver.	18	19	20	Aver.
Viburnum affine var.	150.1	18.8	23.8	64.2	99.4	73.8	15.6	62.9
hypomalacum	100	70	70	80	100	80	50	76.7
Polycodium spp.	36.3	88.1	68.4	64.3	12.5	190.6	126.9	110.0
	70	100	90	86.7	50	60	80	63.3
Viburnum prunifolium	3.2	1.2	3.7	2.7	3.7	8.1	3.8	5.2
	20	20	40	26.7	50	50	40	46.7
Chionanthus virginica	5.6		3.8	3.1	6.2	0.6	0.6	2.5
	30		60	30	50	10	10	23.3
Crataegus sp.	5.1			1.7	0.6			0.2
	40			13.3	10			3.3
Rosa virginiana	10.6			3.5	10.0	7.5	5.0	7.5
	30			10	50	20	20	30
Styrax grandifolia	5.1			1.7	2.5			0.8
	20			6.7	20			6.7
Ceanothus americanus	1.3			0.4	1.3	1.9		1.1
	10			3.3	10	10		6.7
Evonymus americanus	1.3			0.4	31.4			10.5
	10			3.3	60			20
Amelanchier canadensis	0.6	3.2	0.6	1.5				
	10	40	10	20				
Ilex opaca		0.6		0.2				
		10		3.3				
Vaccinium spp.			33.1	8.3	23.1	0.6		7.9
			70	23.3	30	10		13.3
Viburnum acerifolium			3.7	1.2				
			20	6.7				
Azalea nudiflora					21.6			7.2
					30			10
Viburnum rufidulum					1.2			0.4
					20			6.7
Lianas								
Vitis aestivalis	5.0	1.9	1.3	2.7				
	50	20	20	30				
Parthenocissus quinquefolia	5.0		2.5	2.5	3.1			1.0
	20		10	10	30			10
Tecoma radicans	1.3			0.4				
	10			3.3				
Smilax glauca	3.1			1.0				
	10			3.3				
Vitis rotundifolia	4.4			1.7	46.9			15.6
	30			10	90			30
Rhus toxicodendron	4.4		0.6	1.7	1.3			0.4
var. *radicans*	10		10	6.7	10			3.3
Smilax rotundifolia		1.3	1.3	0.9	0.6	3.1	0.6	1.4
		40	20	20	10	10	10	10
Vitis labrusca			0.6	0.2				
			10	3.3				
Lonicera sempervirens					4.4	2.5		2.3
					30	10		13.3
Bignonia capreolata					2.5			0.8
					10			3.3

localized occurrence indicated for *Ceanothus americanus* seem to undervalue its distribution in hardwood stands of the region.

The counts for lianas are too erratic to merit detailed discussion. All of the species are more common in lowland forests, all probably appear irregularly everywhere in upland hardwoods. The values for *Vitis aestivalis* may be such that the species should be considered a part of the white oak type. It would also appear that *Smilax rotundifolia* may be expected in small numbers in any upland hardwood stand.

It is of interest that the total density of all these woody subordinates averages more than 50% greater in the post oak than the white oak stands.

Herbs.—In the sampling of all of the oak-hickory stands thirty-seven species of herbs are recorded (Table 21). Of these, eleven species are found in both the white and post oak types, nineteen occur only in the post oak and seven only in the white oak. It might be concluded therefore that one group of species is characteristic of all upland climax hardwood and that the two types of hardwood each have a distinctive additional group of species. In spite of the data this is probably only partially true. The data must be interpreted in terms of field experience.

It is probable that any of the eleven species found in both types may be found in any upland oak-hickory stand. However, these should not be considered as typical of, or restricted to such stands for *Potentilla canadensis* and *Euphorbia corollata* are ubiquitous weeds of field, roadside and pineland. Most of the other species may be found in other than oak-hickory environments although usually associated with mature forest stands. The seven species found only in the white oak stands are also characteristic of mature forest communities. It seems strange that some of them were not found in the post oak type. The ten species recorded only from the post oak community are certainly not restricted to the type. In fact, the majority of them are found more abundantly along margins of mature woods, stable roadsides and old fence rows. However, where they are most abundant they are usually in partial shade. Perhaps the less complete crown cover in the post oak type favors their better growth and the shading of white oak excludes them. It seems entirely possible that *Prunella vulgaris, Asarum virginicum, Ascyrum hypericoides, Coreopsis major* and *Seriocarpus* spp. might be found in the white oak type. *Strophostyles umbellata, Lespedeza repens* and the two species of Aster suggest full sunlight and probably disturbance of the habitat. This conception may be affected by observation of these species where competitive relationships are disturbed by man. Perhaps the hardwood forest is their normal environment.

Taken collectively the list of herbs for post oak suggest a drier and possibly a poorer site than does the list from white oak stands.

The total herb density for white oak stands is 120 for 18 species compared to 265 for 30 species in post oak, which gives a mean density for species of 10.9 and 8.8 respectively.

Among the 37 species found in oak stands there are 11 that are also found

TABLE 21.—Density and frequency of herbs found in climax upland hardwood stands.

	White Oak Series				Post Oak Series			
Series	15	16	17	Aver.	18	19	20	Aver.
Chimaphila maculata	72.5	72.5	45.0	63.3			12.5	4.2
	40	50	60	50			10	3.3
Desmodium nudiflorum	17.5	15.0	25.0	19.2				
	30	40	50	40				
Grass spp.	17.5	5.0	5.0	9.2	42.5	12.5		18.3
	30	20	20	23.3	60	20		26.7
Hieracium gronovii	2.5	2.5		1.7		57.5	22.5	26.7
	10	10		6.7		40	30	23.3
H. venosum	5.0			1.7		35.0	12.5	15.8
	20			6.7		50	20	23.3
Panicum sp.	7.5			2.5	30.0	10.0	15.0	18.3
	10			3.3	30	10	20	20
Carex sp.	2.5			0.8	22.5	2.5	5.0	10.0
	10			3.3	50	10	10	23.3
Galium pilosum	12.5			4.2	5.0	2.5		2.5
	20			6.7	20	10		10
Agrimonia gryposepala	7.5			2.5	2.5			0.8
	10			3.3	10			3.3
Aristolochia serpentaria	2.5			0.8	10.0			3.3
	10			3.3	30			10
Aureolaria flava	2.5			0.8				
	10			3.3				
Potentilla canadensis		10.0		3.3	12.5	45.0	12.5	23.3
		30		10	10	40	10	20
Uvularia sessilifolia		2.5		0.8				
		10		3.3				
Desmodium obtusum		2.5		0.8				
		10		3.3				
D. laevigatum		2.5	5.0	2.5				
		10	10	6.7				
D. dillenii			5.0	1.7				
			10	3.3				
D. rotundifolium			7.5	2.5				
			10	3.3				
Euphorbia corollata			5.0	1.7	5.0	5.0	2.5	4.2
			10	3.3	20	10	10	13.3
Panicum microcarpon					17.5	25.0	10.0	17.5
					40	30	20	30
Scutellaria sp.					2.5	17.5		6.7
					10	20		10
Strophostyles umbellata					2.5	5.0		2.5
					10	10		6.7
Prunella vulgaris					2.5			0.8
					10			3.3
Asarum virginicum					50.0			16.7
					50			16.7
Galium circaezans					7.5			2.5
					10			3.3
Pycnanthemum flexuosum					7.5			2.5
					10			3.3
Andropogon virginicus						75.0	85.0	53.3
						80	50	43.3

TABLE 21.—(Continued)

	White Oak Series				Post Oak Series			
Series	15	16	17	Aver.	18	19	20	Aver.
Aster ericoides						5.0	5.0	3.3
						10	20	10
Lespedeza repens						10.0	15.0	8.3
						10	10	6.7
Ascyrum hypericoides						2.5		0.8
						10		3.3
Cunila origanoides						2.5		0.8
						10		3.3
Coreopsis major						5.0		1.7
						10		3.3
Solidago nemoralis						12.5		4.2
						20		6.7
Tephrosia virginiana							17.5	5.8
							10	3.3
Chrysopsis mariana							2.5	0.8
							10	3.3
Aster dumosus							2.5	0.8
							10	3.3
Seriocarpus linifolius							5.0	1.7
							10	3.3
S. asteroides							20.0	6.7
							20	6.7

in upland loblolly pine stands (see Table 4). Most of these appear in several age classes of pine and, when this is true, density and frequency of the herbs declines with increase of age of pine. With the single exception of *Chimaphila*

Fig. 17. Climax forest (white oak type) on good upland soil. Fig. 18. Postclimax forest on low rich flood plain. Large willow oak at left, shagbark hickory at right.

maculata their numbers are still smaller in oak-hickory. All eleven of these species may be thought of as rather characteristic of woodland, pine or hardwood. However, *Chimaphila maculata, Hieracium gronovii, Galium pilosum, Potentilla canadensis,* and *Euphorbia corollata* are probably ubiquitous for they all are recorded in four to six ages of pine and three or more hardwood stands.

B. POSTCLIMAX

Postclimax (Clements, 1936) implies somewhat more favorable moisture conditions than afforded by the general climate. Of necessity, such conditions can result only under local physiographic or edaphic variations and, in the Piedmont, especially favorable moisture conditions are only associated with streams. The limited extent of Piedmont flood plains as well as disturbance by man or natural forces restrict the mature postclimax vegetation to isolated areas and then, commonly, stands are not extensive or well developed.

Stable talus slopes or abruptly rising banks above moist flood plains are the most common postclimax sites free from disturbance. Here postclimax species may commonly be found but always in small numbers and usually in a narrow strip extending along the stream. Above this strip will be characteristic bluff vegetation and below it, on the flood plain, will be successional communities related to man's activities or controlled by erosion or aggradation by the stream. Obviously such a restricted zone should not be taken as a fair sample of postclimax even though its species composition may be repeated again and again. Since the zone is almost invariably slightly above the level of the general flood plain it is reasonable to suppose that it is slightly less mesic than the flood plain proper. Also, the invariably rising ground above it must affect aeration, run-off, wind and sun exposure and other factors. At this point it would seem advisable to mention that the indicator species for the zone is beech *(Fagus grandifolia)* and that any or all of the species mentioned later may be found here as well, although never in profusion.

North of Durham the Eno River has meandered considerably forming fairly extensive flood plains through which it has more recently cut down leaving broad alluvial terraces. With a minimum of drainage these rich terraces form excellent agricultural land and almost without exception they have consequently been cleared for farming.

For some reason a tract about 50 acres in extent was not cleared. Even cutting[9] was kept at a minimum and many trees seem to be 300 years old or more while most overstory individuals are 100 years old (Fig. 18). The mesic habitat and the vegetation it supports can only be interpreted as postclimax for the region. The stand contains some extremely large trees and, taken as a whole, it is the least disturbed, best developed hardwood stand seen in the area.

The forest was first sampled with the same procedure and numbers of quadrats used in all other stands of this study. However, because of size and

9 February, 1941—Clear cutting has been started and more than half the stand is now gone.

TABLE 22.—Density and frequency of trees in four size classes of postclimax forest.

	Trees		Reproduction	
	Over story	Under story	Trans-gressives	Seed-lings
Quercus phellos	.95	.55		3.3
	45	20		35
Liquidambar styraciflua	.65	1.1	6.8	7.5
	45	45	30	40
Quercus rubra var. *pagodaefolia*	.55	.2	1.3	15.0
	30	20	5	45
Q. alba	.25	.15	.60	1.9
	25	10	10	10
Pinus taeda	.30			
	25			
Nyssa sylvatica	.10	.05	6.3	5.6
	15	5	30	40
Carya ovata	.15	1.1	?	?
	10	40		
Quercus lyrata	.15			1.8
	10			5
Carya carolinae-septentrionalis	.10		?	?
	10			
Acer rubrum	.10	.75	6.9	17.5
	5	40	35	55
Acer floridanum	.05	2.8	36.9	38.6
	5	75	90	95
Celtis occidentalis	.05	.10	2.4	5.8
	5	10	20	20
Quercus velutina	.05			
	5			
Ulmus americana	.05	.30	8.2	34.3
	5	25	75	75
Quercus stellata	.05			
	5			
Cornus florida		1.9	8.8	14.4
		50	35	55
Ilex decidua		.80	5.0	4.4
		40	45	45
Ulmus alata		.75	4.3	5.3
		35	25	15
Carpinus caroliniana		.40	3.7	4.3
		20	25	30
Juniperus virginiana		.35		1.3
		30		10
Morus rubra		.25	.30	.30
		25	5	5
Fraxinus americana		.20	3.8	2.5
		15	40	30
Quercus rubra		.10		
		5		
Carya glabra		.05	?	?
		5		
Prunus serotina			.30	.6
			5	10
Carya spp.			11.3	15.6
			65	80

resulting wide spacing of trees, it seemed highly possible that such a series might be inadequate. Consequently a second complete series was run. Comparison of the two sets of data showed a remarkable constancy in the values for all dominant and subdominant species, as well as for dependents with high densities and frequencies. The data as presented are therefore based upon 20 quadrats for each size class. This gives a lengthened list of subordinate species and at the same time densities and frequencies of many less common species are reduced by half, which is probably nearer their true significance.

The statistics for species of trees are given in Table 22. Density and frequency values are listed successively for each species as it occurred in the overstory, understory, transgressive and seedling strata.

Fifteen species are listed in the overstory. Of these, the first four, willow oak, red gum, swamp red and white oak make up about 66% of the density and likewise have the highest frequencies. Because of the exceptional size of many overstory individuals and consequent wide spacing, no species have very high frequencies or densities. These same factors result in an irregular pattern of cover in the overstory which serves to explain certain apparent inconsistencies in the species list.

In the discussion of flood plain succession it is shown that red and black gum are characteristic successional trees. To find them in the postclimax overstory necessitates some explanation. Because these species are shade tolerant they hold an important place in the subordinate strata and since they are relatively short-lived, individuals rarely attain great age or size. Those counted in the overstory are invariably tall trees with trunks no more than 8-10 inches in diameter and slender spire-like tips reaching up between the broad, rounded tops of oaks and other species. Thus, although their counts are fairly high their effects as a part of the dominant stratum can be materially discounted. *Pinus taeda is,* of course, another successional species. Its position here must be the same as that of pine found in the climax forest on the uplands. Wherever overmature hardwood trees are dead or have fallen several pines can be found in the opening which results. No such area fell in the sample plots and consequently no pine reproduction is recorded, for the shade intolerance of pine excludes it elsewhere. Since every counted individual towered high above the hardwood overstory and still appeared to be younger than the general age of the mature hardwoods in the stand, it can reasonably be assumed that these pines are a normal part of the stand. They must originate in openings and then make such rapid height growth that a few individuals exceed and survive the encroaching hardwoods.

Of the remaining overstory species, black oak and post oak must be incidentals since they appear in none of the lesser size classes and are otherwise typical of uplands. Southern shagbark hickory probably could be similarly classified. The presence of white oak in relative abundance is to be expected because of its adaptation to a far wider range of moisture conditions.

The counts and distribution of these overstory species in the understory substantiate the generalizations above. The general trend is for numbers to

increase with decreasing size classes, which, of course, indicates continuous survival of the species and ready replacement when overstory individuals drop out. It may be significant that all the important overstory oaks are represented in the understory by about half as many individuals with a much reduced frequency. Those species which appear sporadically in the overstory tend to have relatively high numbers and more uniform distribution in the understory.

Acer floridanum exceeds all other species in density and frequency in the understory as well as in the lesser size classes. Even though largely restricted to the understory, individuals of mature tree size appear so regularly that it seems reasonable to describe this postclimax stand as oak-hickory-hard maple.

Nine species are recorded as never attaining overstory status. Of these, southern red oak and pignut hickory are probably only incidental trees. The other seven species may be taken as a fair representation of the lesser understory. They appear mostly as a subordinate or third stratum rather distinct from the dominant layers of the overstory species. None are dependents but all are highly shade tolerant. All are represented by numerous individuals of exceptional size and this is particularly true of dogwood, holly, and ironwood.

The counts for the reproductive strata are rather self explanatory. Almost invariably seedling density is five to ten or more times greater than that of mature individuals of the same species and frequency too declines with increase in age and size. Seedlings of *Acer floridanum* are more than twice as numerous as any other species except American elm. However, the survival of hard maple is apparently far better than elm and furthermore maple mortality is greatest at a later age. As a result, hard maple is the predominating species of the transgressive stratum (about 35% of all transgressives) while elm is relatively inconspicuous (about 8%).

It should be mentioned that, although absent from the quadrats, several swamp chestnut oak *(Q. prinus)* of tree size were seen in the stand and that locally *Ostrya virginiana* and *Diospyros virginiana* were present especially in the lesser understory.

TABLE 23.—The occurrence of shrubs and lianas in postclimax forest as indicated by density-frequency counts.

Rubus spp.	13.8 30	*Parthenocissus quinquefolia*	69.4 100
Viburnum affine var. *hypomalacum*	9.4 55	*Bignonia capreolata*	22.8 80
Viburnum prunifolium	7.1 55	*Smilax rotundifolia*	11.9 75
Vaccinium sp.	3.1 10	*Vitis rotundifolia*	4.6 45
Evonymus americanus	1.9 15	*Tecoma radicans*	3.8 15
Rosa palustris	0.6 10	*Gelsemium sempervirens*	2.8 10
Rhus toxicodendron var. *radicans*	190.1 95	*Smilax bona-nox*	0.6 5
Lonicera japonica	156.8 50		

Shrubs and Lianas.—Lesser woody species are few (Table 23). Five shrubs are listed and of these only *Viburnum prunifolium* and *V. affine* var. *hypomalacum* are fairly abundant and uniformly present. Both *Vaccinium* spp. and *Rosa palustris* are found only locally on slightly raised areas.

Woody climbers however, are exceptionally abundant and rather uniformly distributed throughout the stand. Poison ivy forms great tangles in some parts. It and cross-vine, in several instances, climb to the tops of the tallest trees. These vines are often 3-6 inches in diameter at the base and often the mass in the tree crown is great enough to kill the tree.

Herbs.—The list of herbs is long and heterogeneous (Table 24). Only a few have high density values and still fewer have high frequencies. Obviously the herbs are few in number and at the same time diverse in species. Since more than half the species appear with a frequency of 5% the localization is especially emphasized. Only *Galium tinctorium* is uniformly distributed while an undetermined grass is quite general as are several species of violets.

The list as a whole suggests low, moist, rich, mature woods. Almost with-

TABLE 24.—Density and frequency of herbs in postclimax forest.

Galium tinctorium	127.5 95	*Panicum* sp.	6.3 10
Grass (unknown)	92.5 55	*Carex typhina*	5.0 5
Viola spp.	87.5 45	*Solidago* sp.	3.8 5
Asarum virginicum	80.0 20	*Scutellaria integrifolia*	2.5 5
Carex spp.	43.0 20	*Juncus effusus*	2.5 5
Carex tribuloides	40.0 20	*Luzula carolinae*	2.5 5
Potentilla canadensis	33.8 20	*Phryma leptostachya*	2.5 5
Impatiens biflora	32.5 25	*Aristolochia serpentaria*	2.5 5
Anemonella thalictroides	22.5 5	*Ruellia caroliniensis*	2.5 5
Asarum arifolium	17.5 15	*Aster* sp.	2.5 5
Carex virescens	11.3 10	*Desmodium* sp.	1.3 5
Goodyera pubescens	10.0 20	*Ranunculus recurvatus*	1.3 5
Oxalis stricta	10.0 5	*Prunella vulgaris*	1.3 5
Scutellaria serrata	8.8 5	*Hystrix patula*	1.3 5
Arisaema triphyllum	7.5 20	*Verbena urticaefolia*	1.3 5
Zizia aurea	6.3 15	*Pilea pumila*	1.3 5
Podophyllum peltatum	6.3 5		

out exception the species are shade loving. A few are more typical of wetter sites and some of rich mature woods on drier sites. *Pilea pumila, Ranunculus recurvatus, Juncus effusus, Carex typhina* and *Impatiens biflora* are all species of swampy habitats. *Potentilla canadensis* and *Oxalis stricta* are more common in upland woods. Since the site is relatively low with numerous shallow depressions that are poorly drained the peculiar mixture of species becomes explainable in terms of moisture as related to a few inches difference in elevation.

Because of the dense shade produced by the several heavy strata of woody species the summer flora is undoubtedly reduced in these rich woods. This study was made in June when all woody species had leafed out. In the early spring, this rich forest floor has an entirely different aspect when not flooded, for many other species are then abundant which by June have completely disappeared.

General Considerations.—Slight variations in the perfection of drainage result in quite different moisture conditions in flood plains and bottomlands of the lower Piedmont and even greater differences in the coastal plain. These differences may be reflected in the vegetation type to a marked degree. The subclimax cypress and gum swamps of the coastal plain may be cited as familiar examples resulting from different periods of flooding. For the same reasons, but less obvious during the growing season, soil moisture must differ from site to site in mesic lowlands. These soil moisture differences must be reflected in the composition of the postclimax forest.

The stand described above was completely lacking in beech. Elsewhere, invariably in better drained areas, beech may be found as an important element in postclimax forest. Ashe (1922) mentions almost pure stands of beech on flats around the southern edge of the Dismal Swamp in North Carolina and similar forests containing large proportions of beech in other portions of the Gulf states. Never in very extensive stands but recurring frequently in well-drained lowlands throughout the Coastal Plain and Piedmont, beech may be found with hard maple as one of the usual associates. Wells (1924, 1928) considered the community to be climatically controlled and described it as climax for the area. Evidence is lacking to support this contention. It is more logical to think of the widespread upland oak-hickory communities as the climatic climax. Then, since the various combinations of lowland oaks and hickories with hard maple and beech occur, without exception, in edaphically more favorable habitats, they can only be considered as postclimax.

Within the limits of the range of moisture conditions producing postclimax forest, beech will be more important on the better-drained relatively drier sites. Nearer the wetter end of the range, beech may be entirely lacking and moist site oaks will be relatively more important. Regardless of this variation the entire complex must be recognized as postclimax.

C. PRECLIMAX

The post oak-black jack oak type has a very limited extent. It comprises about 1% of the area of mature upland hardwoods on Duke Forest and this

value is probably representative of most of the region. Its occurrence is almost invariably associated with the poorest soil conditions, either as to soil type or extreme erosion.

When the type is associated with erosion it varies in composition and its permanence will be only relative. With stability the habitat will eventually improve and there is sufficient evidence to indicate that the climatically controlled oak-hickory communities may finally supersede the inferior type. Post oak-black jack oak under these conditions must be considered as subclimax.

However, the community may regularly be found on Orange (Fig. 19), Iredell or closely related soils which have not been eroded or disturbed. These poor soils are usually characterized by a highly impermeable clay layer at a depth of a few inches. Below this layer the soil is permanently dry. This, combined with the physical resistance of the clay stratum, tends to restrict root systems to the shallow surface soil. In the spring these surface strata may be saturated for weeks. As the summer progresses evaporation and drainage from the surface

Fig. 19. Preclimax forest of blackjack and post oak on a poor upland site (Orange soil).

as well as absorption by plants desiccates the soil and species surviving there annually undergo extended periods of drought. Again, the community invariably occupies those sites where only a thin mantle of soil overlies solid rock, another xeric habitat to which the above generalizations apply equally. No change in the edaphic conditions of either habitat can be anticipated. The vegetation, where undisturbed, must be regarded as preclimax.

The preclimax post oak-black jack oak community forms a very open and quite irregular stand. Growth is extremely slow. The trees tend to be gnarled and scrubby, rarely exceeding 30 feet in height and many are much smaller. There is no closed canopy (see Fig. 6, Korstian and Coile, 1938) and consequently distinct strata are not developed as in better stands.

Post oak and black jack oak predominate among the trees, and hickories (mockernut and pignut) are present in some abundance. In addition a surprisingly miscellaneous group of tree species may be present although with little evidence of constancy. Several other upland oaks may be found although, of these, white oak is commonest. Scattered pines of any local species are characteristic but of low frequency and density. Black gum, willow oak and ash may be found in small numbers. Red cedar is the most abundant of the lesser species and often individuals may be relatively large, reaching into the overstory level. Dogwood is always present but forms no closed understory stratum and persimmon is a common associate.

Shrubs are infrequent and species occur with no degree of constancy. Almost any upland hardwood species may be found.

The ground cover is characteristic and distinctive because of the paucity of herbs and the extensive mats of mosses and lichens. Large areas are solidly covered with *Dicranum condensatum* and some *D. scoparium*. These moss mats are irregular patches of bare mineral soil, especially during the summer and fall.

The commonest herb is *Danthonia spicata* which is rather evenly distributed. Other species occur sporadically and include weeds of field and roadside such as *Aster dumosus, Lespedeza* spp., *Stylosanthes biflora, Andropogon scoparius,* and *Oenothera fruticosa.* Several grasses may be found but usually as isolated individuals. The composites are particularly noticeable in the fall and they include species of open woodlands such as *Seriocarpus linifolius, Liatris graminifolia, Chrysopsis mariana,* and *Solidago* spp.

Life Forms

The list of species in the appendix was compiled directly from the manuscript to make available a ready reference to authorities and common names. Since the manuscript was written without any consideration of growth forms whatsoever and all major communities are described, it may be assumed that the species mentioned comprise a reasonably representative sample of the entire flora. To be sure, seasonal variation is not well represented and the lists for each habitat are in no instance intended to be complete. This means that species which are conspicuous because of size, numbers, or rarity may be over-

emphasized. Thus it is certain that trees and shrubs as well as pteridophytes are much more completely listed than other groups, e.g., grasses or sedges.

An attempt at life form classification was made in spite of these limitations since it might at least give suggestive information. As indicated by symbols (appendix) the life form of each species was determined according to the rather generally accepted system of Raunkiaer (1934). The groupings are based upon the position of the buds of a plant during the unfavorable season of the year. Those plants with greatest bud protection have been shown to predominate in least favorable climates.

The buds of trees and shrubs *(phanerophytes)* are least protected and species of this type predominate in tropical floras. Buds of *chamaephytes* are in or at the surface of the ground during unfavorable seasons and this group represents an increasingly large percentage of the flora with increasing distance from the tropics. In the same manner, *hemicryptophytes,* whose buds lie dormant just beneath or in the soil surface, increase from the tropics to temperate climates where the group predominates. *Cryptophytes* are particularly adapted to extreme conditions because of their deeply buried buds and stored food (e.g., bulbs). Finally those plants which are dependent only upon seeds for survival *(therophytes)* are best protected of all groups against cold or heat and their numbers are only limited by the ability of species to complete their life cycle during the favorable season.

These are the major categories of Raunkiaer's system. More detailed subdivision would seem to be out of place in such an exploratory study. No attempt is here made to distinguish introduced species for, as suggested by Raunkiaer, if they have found a permanent place in a flora without the continued help of man, they must be of the same general life form plan as the indigenous species and probably affect the spectrum but slightly.

Raunkiaer's *normal spectrum* is an expression of the life form distribution among a randomly selected group of species from the flora of all the world. When a regional spectrum is determined, at least one of the life form percentages will invariably exceed the percentage of that group in the normal spectrum. This outstanding group is the real measure of the selective nature of the sum total of environmental factors involved and the climate can thus be termed Chamaephytic or Hemicryptophytic, etc., as the case may be.

On this basis and using the life forms indicated in the species list as a sample of the Piedmont flora, the climate must be hemicryptophytic for hemi-

	No. of spp.	Percentage distribution of spp.					PTER.
		PH	CH	H	CR	TH	
Piedmont	387	29.7	1.6	45.0	11.3	12.4	16.8:1
Normal spectrum	.....	46	9	26	6	13	25:1

cryptophytes far exceed all other life forms in the flora and their value strongly exceeds that of the group in the normal spectrum. The low percentage of chamaephytes and relatively high percentage of cryptophytes are, as Raunkiaer has shown, typical of temperate climates (see also several spectra in McDonald,

1937). When the Piedmont spectrum is compared with those of other temperate regions, the predicted weaknesses of the sample seem to be supported. The hemicryptophyte percentage is probably lower than it should be and the phanerophytes are probably somewhat overemphasized. Temperate floras usually have a higher proportion of pteridophytes than the ratio of 25:1 indicated by the normal spectrum but a ratio of 16.8:1 (pteridophyte quotient 1.5) suggests that the pteridophytes are probably more completely listed than spermatophytes.

With each additional study of life forms it becomes increasingly apparent that Raunkiaer was correct when he contended that the complex of life forms of a region is the product of all the environmental factors affecting vegetation and that a series of spectra may be a means of evaluating and comparing environments. On a regional basis a close correlation can be shown between spectra and climatic factors. Areas of similar precipitation-temperature relationships marked by isotherms or some similar indicator are closely matched by biochores or lines of equal life form dominance. Altitudinal zonation produces the same spectrum changes as latitudinal zonation.

Within a climatic region local conditions in the environment, usually edaphic or physiographic, may vary so widely as to produce strikingly different vegetation types in close proximity. Less extreme differences are recognized even in climax vegetation which are designated as post- or preclimax communities. How closely related these communities are or how divergent the extremes of their effective environments may be, could as well be indicated by life form spectra as can the differences in regional floras. Perhaps such spectra could be as useful as those of regional floras. Withrow (1932) determined the spectra of four widely differing communities in the Cincinnati region and was able to show correlations with the geographic ranges of the major species in each community. Her findings might have been more effective could she have had a basic regional spectrum for comparison.

The climax forest of a region would be expected to grow under conditions far more favorable than those of the region as a whole and the more favorable environment should be reflected in its spectrum. The climax forest of the Piedmont is hemicryptophytic by comparison with the normal spectrum but, judging by conclusions drawn from regional studies, its environment provides a highly favorable moisture-temperature relationship. The climax phanerophyte percentage is double that of the regional value. This substantiates what we already know but also suggests the consideration of other communities. Unex-

	No. of spp.	Percentage distribution of spp.				
		PH	CH	H	CR	T
Preclimax	27	48.1	0	44.4	3.7	3.7
Postclimax	86	50.0	0	41.8	5.8	2.3
Climax	89	59.6	0	36.0	4.5	0
Piedmont	387	29.7	1.6	45.0	11.1	12.4
Normal	....	46	9	26	6	13

pectedly the postclimax and preclimax spectra are remarkably similar to each other and both differ from the climax in the same manner. Both suggest an environment slightly less favorable to phanerophytes than the climax. Both are more strongly hemicryptophytic and both include a low percentage of therophytes. The preclimax spectrum might be much modified by a more thorough study of the lesser vegetation in the community. The postclimax spectrum would probably change only slightly with the addition of species, for only the spring herbs of the forest floor are not included here. What do these spectra mean then? Obviously a climax spectrum is distinct from its regional spectrum but to what extent are the life forms of regional climax variations interrelated?

The spectra for bluff vegetation express the environmental extremes of the habitats as well as how radically these communities may differ from the vegetation of the region as a whole. The spectrum for the northfacing bluff is apparently quite unorthodox for the percentages suggest that the flora is cryptophytic. No cryptophytic climate is recognized by Raunkiaer or suggested by more recent investigators. Can it be that cryptophytes regularly reach this degree of importance (4.6 x normal) in such situations within hemicrypto-

	No. of spp.	Percentage distribution of spp.					PTER.
		PH	CH	H	CR	TH	
S-facing bluff	45	26.6	0	51.1	4.4	17.8	6.4:1
N-facing bluff	84	45.2	3.6	25.0	27.4		10.5:1
Piedmont	387	29.7	1.6	45.0	11.1	12.4	16.8:1
Normal	....	46	9	26	6	13	25:1

phytic climatic areas? To be sure they increase with latitude and altitude and these bluffs have a decidedly northern complex of species. Northern affinities are further indicated by the decrease of hemicryptophytes to a percentage slightly below normal. In the same sense the increase of chamaephytes over their regional value may be significant within a hemicryptophytic climatic area. The habitat seems to be favorable to phanerophytes but not relatively as favorable as climax situations within the region.

The spectrum of the south facing bluff suggests a therophytic or semi-desert flora although remaining essentially hemicryptophytic. The extreme conditions of temperature, moisture and soil favor the special characteristics of therophytes with their rapid growth and maturation as well as the resistant seed form of dormancy. With such contrasts in spectra it is obvious that the greatest diversity of the regional flora is concentrated along the bluffs of the larger streams.

From the available quadrat data spectra were determined for several series of successional communities. Certain spectral characteristics would be anticipated in any such series. Cultivated fields and disturbed areas are known to be characterized by annual vegetation. Communities dominated by trees should have much more stable environments and consequently have spectra whose characteristics approach those of the regional spectrum. Trends should be

apparent in the shifting of life form percentages from old fields through successional stages which follow. Therophyte percentages should decrease, hemicryptophytes should increase and phanerophytes should increase. How rapidly these changes might take place and how the shifting percentages might adjust themselves before stabilization in the climax was unknown.

The tabulation of spectra for a successional series of old field stands shows the one-year field dominated by therophytes and, except for a low percentage of phanerophytes, an associated spectrum suggesting a desert flora. A steady decline of therophytes in the early years of succession terminates in their elimination relatively soon after tree dominance is established. The anticipated trends for hemicryptophytes and phanerophytes are apparent but with peculiar

Age of stand	No. of spp.	Percentage distribution of spp.				
		PH	CH	H	CR	T
1 year	35	2.9	8.6	22.9	8.6	57.1
2 years	64	1.6	4.7	40.6	10.9	42.2
3 years	39	2.6	7.7	43.6	10.3	35.9
11 years	49	32.7	0	49.0	6.1	12.2
22 years	53	62.3	0	32.1	5.7	0
31 years	48	72.9	0	22.9	4.2	0
34 years	53	56.6	0	41.5	1.9	0
42 years	37	59.5	0	32.4	2.7	2.7
70 years	54	64.8	0	31.5	3.7	0
110 years	61	75.4	0	19.7	4.9	0
Climax	89	59.6	0	36.0	4.5	0
Normal		46	9	26	6	13

irregularities which suggest a rhythmic variation. These fluctuations are not easily explained. By the second year the flora is unquestionably hemicryptophytic for the group here exceeds its percentage in the normal spectrum. Hemicryptophytes reach their peak in the 11-year pine stand where their percentage even exceeds the regional value. This must result from the still abundant presence of old field hemicryptophytes and the additional appearance of species characteristic of the forest. As the stand increases in age percentages of hemicryptophytes decline, then rise abruptly at middle age and again decline slowly to a value below the normal when the stand is overmature. Approaching the climax there is again an increase.

Values for phanerophytes increase to an exceptional high in middle age, then decline abruptly and again rise steadily to another high in overmaturity. The 31-year high suggests a peak in diversity of woody species for normal stands. The 110-year peak may be related to the presence of pineland species soon to be eliminated and the entrance of species of hardwoods soon to predominate. A steady decline to climax is indicated. These two peaks for phanerophytes exceed those listed for some tropical floras and seem significant since hemicryptophytes are in both instances well below normal. Probably they are related to the homogeneity of the community and the selective nature of a well

developed pine stand upon its associated species. Perhaps new standards are necessary for considering life form characteristics of relatively small and uniform forest areas within a region of diverse communities.

Spectra for successional stands of bottomland pine show some of the same characteristics. This series is less complete but a peak for phanerophytes is indicated at middle-age (34 years) and a second still higher peak in overmaturity (90 years). As before, postclimax shows a drop to a value approach-

PINE	No. of spp.	Percentage distribution of spp.				
		PH	CH	H	CR	T
15 years	45	53.3	2.2	35.6	2.2	6.7
18 years	54	50.0	1.9	33.3	5.6	9.3
34 years	41	75.6	0	24.4	0	0
45 years	51	68.6	0	27.5	3.9	0
90 years	54	77.8	0	16.7	5.6	0
Post-climax	86	50.0	0	41.8	5.8	2.3
36 years	41	78.0	0	17.1	0	4.9
14 years	48	60.4	0	31.3	4.2	4.2
6 years	48	37.5	0	45.8	6.3	10.4
BIRCH						

ing the regional phanerophytes. Similarly hemicryptophytes are high in the young stand, decline, rise and decline again to an exceptional low in overmaturity. Postclimax hemicryptophytes approach the regional value. Surprisingly, spectra for a short series of birch stands suggests that the same rhythm may proceed with succession there.

The data upon which this discussion is based were obtained with other objectives in mind. Their adequacy for such a discussion has not been demonstrated. It is felt, however, that several considerations justify this attempt at life form analysis of community data. With increasing knowledge it may be possible to use community spectra to advantage for evaluating local environmental conditions within a regional vegetation type. Several provocative questions remain to be answered after this preliminary approach to such comparisons. One concerns the fluctuations in the trend of life form changes associated with succession, and the possibility that these may be constant and predictable. Another refers to the apparent similarity of life forms suggested by the spectra of climax, postclimax and preclimax. This would hardly be anticipated yet it may be the true situation.

Just as it is necessary to use the normal spectrum as a basis of reference in any regional study of life forms, a regional spectrum, as complete as possible, appears to be a necessity for constructive consideration of community spectra.

Summary

1. The Piedmont Plateau is an ancient peneplain lying between the Blue Ridge mountains and the Coastal Plain and extending from Pennsylvania to

Alabama. Soils, topography and vegetation are similar from Virginia southward and the North Carolina portion is representative of the whole.

2. An ecological analysis of the naturally occurring plant communities of the North Carolina Piedmont was undertaken to provide basic information for continued research in ecology and silviculture, and in the hope of contributing to the solution of problems of forest management. Since the entire southern Piedmont is a physiographic and biotic unit the results and conclusions derived from this study are of much more than local significance.

3. The study was aimed at a characterization of all the major plant communities on a qualitative and quantitative basis as well as an interpretation of the major successional trends. To this end quadrat sampling was done in stands of every available age class for each major community. Within each stand five layer-communities or strata were distinguished and sampled separately. These were, the dominant or overstory stratum, the subdominant or understory stratum, the transgressives and tall shrubs, the seedlings and low shrubs, and the herbs. Not less than ten list-count quadrats of appropriate size were done for each stratum in each stand. In addition basal area was obtained for trees. This procedure has made it possible to summarize all statistical data in terms of the two important phytosociological concepts: frequency and density.

4. Uplands and lowlands of the region are ecologically distinct because of the perfection of drainage, high summer temperatures and periodic dry spells. They must then be considered separately. The agricultural history of the region has been such that only inaccessible sites or those of inferior quality are free from disturbance or the effects of man. Most of the plant communities are therefore of secondary origin and their consideration must be kept distinct from the relatively restricted primary communities.

5. Almost without exception upland communities have developed on abandoned fields. They are characterized by a few distinct and easily recognized stages of dominance which regularly succeed each other. Fields abandoned for one year are dominated by *Leptilon canadense* and *Digitaria sanguinalis*. The second year *Aster ericoides* with a mixture of *Ambrosia artemisiifolia* is the important species. By the third year Andropogon (usually *A. virginicus*) is dominant and it maintains itself until shaded out by pine *(P. taeda* or *P. echinata)* whose seedlings may be found among the broom sedge as early as the third year. Pine may overtop the Andropogon by the fifth year and frequently forms closed stands in 10-15 years. Neither of these pines reproduces in its own shade but several hardwoods do. A pine stand is middle-aged by forty years and by then there will have developed a distinct understory of subordinate hardwoods such as red gum, black gum, dogwood and sourwood. In addition several seedling and transgressive oaks and hickories will be present. By 70-80 years the pine is overmature and as it thins out it is replaced by oaks and hickories which have increased steadily in the lesser strata. Eventually (150-200 years) oak-hickory dominance may be attained with scattered pine remaining as relics.

6. Lowland fields may follow a similar pattern if well drained. However, *Rubus* spp. is an important component of the pre-pine stages and is only gradually eliminated after pine dominance. The understory of the lowland pine stands includes many hardwoods and the species of oak and hickory which appear as the stands mature are typical of lowlands. In addition some beech and hard maple *(A. floridanum)* are present. Ultimately all but a few pine are eliminated and replaced by these lowland oaks and hickories with beech and hard maple associated.

7. Secondary communities in bottomlands are variable in composition and dominance. When pine does not come into a field, mixed hardwood stands are not uncommon but the same species may also appear in pure stands. Birch dominance occurs occasionally. By 36 years it has an understory and reproduction which indicate its decadence and that elm, red maple and ash will succeed it. Pure stands of sycamore may develop on lowland fields and sycamore too is replaced by maple-elm-ash in some combination. Young mixed stands may include birch, sycamore, red gum, tulip poplar, and other species. Eventual maple-elm-ash dominance is likewise indicated for these mixed stands regardless of the combination of species. The final community is again lowland oak-hickory.

8. Pine forest does not regenerate on burned and cutover areas. The fast growing subordinate species such as red gum, red maple and many others grow up quickly from sprouts and seed, and pine may be almost completely excluded. Oak and hickory seedlings and transgressives which were present in the old stand likewise profited by the removal of the overstory for they reach tree size and eventual dominance sooner than they would have coming up under the pine.

9. Primary communities are restricted to isolated areas relatively inaccessible to man or valueless for cultivation. The commonest are on small islands and spits formed in streams. On these wet and poorly drained areas the pioneer woody species are willow and alder which frequently form thickets. With stability and drainage the dominants are replaced by birch or sycamore which in turn develop an understory of elm, ash and red maple. The similarity between this and secondary lowland succession is obvious.

10. Bluffs along streams constitute rather mature primary habitats. Because of the variation in exposure, nature of the rock, erosion, etc., there is great diversity in the species present and the degree of development of the plant communities. South facing bluffs have the most xeric habitats in the region and the species are characteristic. Black jack and post oak are common as are several sclerophyllous shrubs, mostly Ericaceae. North facing bluffs are mesic and usually exceptionally favorable habitats. As a consequence they support a great diversity of species among which are a number that are typical of higher and cooler latitudes and altitudes. The rarest species in the region may also be found here.

11. Erosion has played a part in the history of every habitat in the Piedmont. Site quality and ecological development can often be directly correlated

with the degree of erosion. Local extremes result in gullying and the exposure of raw subsoils. Revegetation of these areas is almost impossible unless erosion is checked. Then a ground cover of lichens commonly appears with a scattering of legumes and several other typical small herbs. After a period of stability a sequence of herbs comparable to those of old fields appears and pine eventually occupies the site.

12. Bare rock, another primary habitat, is only of local significance. Except for occasional boulders, which are usually of no ecological importance, rock outcrops are common only along stream margins and in bluffs. Mat formation by mosses and lichens precedes the establishment of communities of higher plants. The rates of this development as well as the species involved are highly variable. Several species, rare or uncommon in the region, may be found associated with rock outcrops on both north and south facing bluffs.

13. The climax of the region is oak-hickory as indicated by relic stands and the gradual development of these hardwoods in the understory of pine stands. The commonest upland oaks are white, black, post, northern red, southern red and scarlet. The commonest hickories are white and pignut. Variations in site may result in variation in the composition of the dominant stratum so that, in general, two oak-hickory climax types may be recognized. The best sites are characterized by a preponderance of white oak with black oak an important associate and other oak species present in smaller numbers. On somewhat less favorable sites post oak is most abundant and white oak is relatively much less important. Black oak is absent from this community but black jack oak, absent from the white oak types, is almost always present here. These variations in the overstory species are the major differences in the two types.

14. Because of the agricultural value of lowlands postclimax vegetation is largely confined to narrow strips of rough talus below north facing bluffs. Data obtained from a single extensive old flood plain correlate well with the observations of species found on talus. The dominants are again oak-hickory with the addition of beech and hard maple. Within the moisture range of the type, beech seems to be favored on the best drained areas and maple on the wettest sites. Willow oak is most abundant, swamp red oak is somewhat less so. White oak is always present and overcup and swamp chestnut oak may be anticipated in small numbers. The hickories are likewise characteristic of low lands and include several species of shagbark as well as bitternut.

15. Preclimax is an oak-hickory community associated with dry south facing bluffs or poor soils characterized by an impervious clay hardpan. Stands are usually ragged and irregular with incomplete crown cover and weak development of understory. The character species are post oak and black jack oak with scattered hickories (mockernut, pignut). Such diverse species as white oak, red cedar, black gum, willow oak, ash and dogwood may be found in association. This development is localized and never of great extent.

16. The life forms of the species mentioned in the text were determined according to the system of Raunkiaer. The flora of the Piedmont is hemicryp-

tophytic with a phanerophytic physiognomy. Spectra were also determined for special communities within the region. All climax communities are hemicryptophytic but phanerophytes are nearly double the percentages for the region. Spectra for bluffs serve to emphasize the extremes of the environments. Cryptophytes apparently predominate on north facing bluffs. Spectra for series of successional communities show definite trends in life form changes but also suggest rhythmic fluctuations in these trends.

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APPENDIX

List of the species mentioned in the text with their authorities and the common names which have been used. The symbols indicate the following life forms:

Phanerophytes
Mega-, Mesophanerophytes—MM
Microphanerophytes—M
Nanophanerophytes—N
Chamaephytes—Ch
Hemicryptophytes—H
Cryptophytes
Geophytes—G
Helo-, Hydrophytes—HH
Therophytes—Th

Trees

Acer floridanum (Chapm.) Pax. MM ..... Hard Maple
Acer negundo L. MM ..... Box elder
Acer rubrum L. MM ..... Red maple
Aesculus neglecta Lindl. var. *georgiana* Sarg. M ..... Buckeye
Aesculus neglecta Lindl. var. *pubescens* Sarg. M ..... Buckeye

Betula nigra L. MM ..... Birch

Carpinus caroliniana Walt. MM ..... Ironwood
Carya alba (L.) K. Koch MM ..... Mockernut hickory
Carya carolinae-septentrionalis (Ashe) Dode MM..Southern shagbark hickory
Carya cordiformis (Wang.) K. Koch MM ..... Bitternut hickory
Carya glabra (Mill.) Spach. MM ..... Pignut hickory
Carya microcarpa Nutt. MM
Carya ovata (Mill.) K. Koch MM ..... Shagbark hickory
Carya pallida (Ashe) Sarg. MM.... ..... Pale hickory
Celtis occidentalis L. MM..... Hackberry
Cercis canadensis L. MM..... Red bud
Cornus amomum Mill. M
Cornus florida L. MM ..... Dogwood

Diospyros virginiana L. MM....Persimmon

Fagus grandifolia Ehrh. MM..... Beech
Fraxinum americana L. MM..... White ash
Fraxinus pennsylvanica Marsh. MM ..... Red ash
Fraxinus pennsylvanica var. *lanceolata* (Borkh.) Sarg. MM ..... Green ash

Ilex decidua Walt. M .....Deciduous holly
Ilex monticola Gray M ....Mountain holly
Ilex opaca Ait. M ..... Holly

Juglans nigra L. MM ..... Black walnut

Juniperus virginiana L. MM ....Red cedar

Liquidambar styraciflua L. MM..Red gum
Liriodendron tulipifera L. MM..... ..... Tulip poplar

Magnolia tripetala L. MM
Morus rubra L. MM..... Red mulberry

Nyssa sylvatica L. MM ..... Black gum

Ostrya virginiana (Mill.) Koch MM ..... Hop hornbeam
Oxydendrum arboreum (L.) DC. MM ..... Sourwood

Pinus echinata Mill. MM....Shortleaf pine
Pinus palustris Mill. MM....Longleaf pine
Pinus strobus L. MM ..... White pine
Pinus taeda L. MM ..... Loblolly pine
Pinus virginiana Mill. MM....Virginia pine
Platanus occidentalis L. MM.....Sycamore
Prunus serotina Ehrh. MM....Black cherry

Quercus alba L. ..... White oak
Quercus borealis Michx. f. var. *maxima* (Marsh.) Ashe MM ..... Northern red oak
Quercus coccinea Muench. MM ..... Scarlet oak
Quercus lyrata Walt. MM....Overcup oak
Quercus marilandica Muench. MM ..... Blackjack oak
Quercus nigra L. MM ..... Water oak
Quercus phellos L. MM ..... Willow oak
Quercus prinus L. MM ..... Swamp chestnut oak
Quercus rubra L. MM....Southern red oak
Quercus rubra var. *pagodaefolia* (Ell.) Ashe MM..... Swamp red oak
Quercus stellata Wang. MM..... Post oak
Quercus velutina Lam. MM ..... Black oak

Salix nigra Marsh. MM..... Black willow
Sassafras officinale Nees and Eb. MM ..... Sassafras

Tsuga canadensis (L.) Carr. MM ..... Hemlock

Ulmus alata Michx. MM.....Winged elm
Ulmus americana L. MM....American elm
Ulmus fulva Michx. MM.....Slippery elm

Shrubs and Vines

Alnus rugosa (DuRoi) Spreng. M..... ..... Alder
Amelanchier canadensis (L.) Medic. M .....Shadbush
Ascyrum hypetricoides L. N
Asimina parviflora (Michx.) Dunal N .....Pawpaw
Asimina triloba (L.) Dunal M....Pawpaw
Azalea nudiflora L. N .....Azalea

Batodendron arboreum (Marsh.) Nutt. M
Benzoin aestivale (L.) Nees M .....Spice bush
Bignonia capreolata L. MM.....Cross vine

Callicarpa americana L. N
Calycanthus fertilis Walt. M
Ceanothus americanus L. N
Cephalanthus occidentalis L. M ..... Buttonbush
Chionanthus virginica L. M.....Fringe tree
Crataegus uniflora Muench. N ..... Hawthorne

Evonymus americanus L. N .....Strawberry bush

Gelsemium sempervirens (L.) Ait. f. MM

Hamamelis virginiana L. M
Hydrangea arborescens L. N

Kalmia latifolia L. M.....Mountain laurel

Leucothoe racemosa (L.) Gray M
Lonicera japonica Thunb. M .....Japanese honeysuckle

Parthenocissus quinquefolia (L.) Planch. MM.....Virginia creeper
Polycodium candicans Small N
Polycodium neglectum Small N
Polycodium stamineum (L.) Greene N

Rhododendron catawbiense Michx. M .....*Rhododendron*
Rhus copallina L. M.....Winged sumach
Rhus glabra L. M.....Smooth sumach
Rhus toxicodendron L. var. *radicans* (L.) Torr. MM.....Poison ivy
Rosa palustris Marsh. N
Rosa virginiana Mill. N
Rubus spp. H (8 spp.).....Blackberry

Sambucus canadensis L. M.....Elderberry
Smilax bona-nox L. M
Smilax glauca Walt. M .....Smilax
Smilax rotundifolia L. M.
Staphylea trifolia L. M
Styrax grandifolia Ait. M.....Styrax
Symplocos tinctoria (L.) L'Her. M

Tecoma radicans (L.) Juss. MM .....Trumpet creeper

Vaccinium spp. M (2 spp.) N (2 spp.) .....Blueberry
Viburnum acerifolium L. N
Viburnum affine Bush var. *hypomalacum* Blake N .....Downy viburnum
Viburnum prunifolium L. M.....Black haw
Viburnum rufidulum Raf. M .....Southern black haw
Vitis aestivalis Michx. MM
Vitis cordifolia Michx. MM
Vitis labrusca L. MM.
Vitis rotundifolia Michx. MM ..... Muscadine grape

Herbs

Acalypha gracilens Gray Th
Achillaea millefolium L. H
Actaea alba (L.) Mill. G
Adiantum pedatum L.
Agrimonia gryposepala Wallr. H
Agrimonia parviflora Ait. H
Allium vineale L. G
Ambrosia artemisiifolia L. Th
Ambrosia trifida L. Th
Amsonia tabernaemontana Walt. H
Andropogon elliottii Chapm. H
Andropogon scoparius Michx. H
Andropogon ternarius Michx. H
Andropogon virginicus L. H .....Broomsedge, Andropogon
Anemone quinquefolia L. G
Anemonella thalictroides (L.) Spach. G
Antennaria fallax Greene Ch
Antennaria parlinii Fernald Ch
Antennaria plantaginifolia (L.) Richards Ch

Anthoxanthum odoratum L. H
Aplectrum hyemale (Muhl.) Torr. G
Arenaria brevifolia Nutt. Th
Arisaema triphyllum (L.) Schott. G
Aristida dichotoma Michx. Th
Aristolochia serpentaria L. G
Aruncus sylvester Kostel. H
Asarum arifolium Michx. H
Asarum canadense L. var. *reflexum* (Bichn.) Robinson H
Asarum virginicum L. H
Asclepias incarnata L. var. *pulchra* (Ehrh.) Pers. H
Asclepias verticillata L. H
Asplenium montanum Willd.
Asplenium platyneuron (L.) Oakes
Asplenium trichomanes L.
Aster dumosus L. H
Aster ericoides L. H .....Aster
Aster laevis L. H
Athyrium asplenioides (Michx.) Desv.
Aureolaria flava (L.) Fernald H

Boehmeria cylindrica (L.) Sw. G
Botrychium virginianum (L.) Sw.

Cacalia atriplicifolia L. H
Camptosorus rhizophyllus (L.) Link
Carex hystericina Muhl. H
Carex lurida Wahl. H
Carex tribuloides Wahl. H
Carex typhina Michx. H
Carex virescens Muhl. H
Cassia chamaecrista L. Th
Cassia nictitans L. Th
Castilleja coccinea (L.) Spreng. H
Centrosema virginianum (L.) Benth. H
Chamaelirium luteum (L.) Gray G
Cheilanthtes lanosa (Michx.) Link
Cheilanthes tomentosa Link
Chimaphila maculata (L.) Pursh H
Chimaphila umbellata (L.) Bart. H
Chrysanthemum leucanthemum L. var. *pinnatifidum* Lecoq. and Lam. H
Chrysopsis mariana (L.) Nutt. H
Cimicifuga racemosa (L.) Nutt. G
Clitoria mariana L. H
Corallorrhiza odontorhiza Nutt. G
Coreopsis major Walt. H
Coreopsis verticillata L. H
Corydalis flavula (Raf.) DC. H
Croton glandulosus L. var. *septentrionalis* Muell. Th
Crotonopsis elliptica Willd. Th
Cunila origanoides (L.) Britton H
Cynodon dactylon (L.) Pers. H
.....Bermuda grass
Cyperus aristatus Rottb. Th
Cyperus compressus L. Th
Cyperus filiculmis Vahl G
Cyperus retrofractus (L.) Torr. G
Cyperus retrorsus Chapm. G.
Cyperipedium acaule Ait. G
Cypripedium calceolus L. var. *pubescens* (Willd.) Correll G
Cystopteris fragilis (L.) Bernh.

Danthonia spicata (L.) Beauv. H
Daucus carota L. H
Desmodium canescens (L.) DC. H
Desmodium dillenii Darl. H
Desmodium laevigatum (Nutt.) DC. H
Desmodium nudiflorum (L.) DC. H
Desmodium obtusum (Muhl.) DC. H
Desmodium rotundifolium (Michx.) DC. H
Diamorpha cymosa (Nutt.) Britton Th
Dianthera americana L. HH
Dicentra canadensis (Goldie) Walp. G
Dicentra cucullaria (L.) Bernh. G
Dicentra eximia (Ker.) Torr. G
Digitaria sanguinalis (L.) Scop. Th
..... Crabgrass
Diodia teres Walt. Th
Diodia virginiana L. H
Dioscorea villosa L. G
Dryopteris hexagonoptera (Michx.) Fee
Dryopteris intermedia (Muhl.) Gray
Dryopteris marginalis (L.) Gray
Dryopteris noveboracensis (L.) Gray

Elephantopus tomentosus L. H
Eleusine indica (L.) Gaertn. Th
Epigaea repens L. Ch
Eragrostis pectinacea (Michx.) Nees Th
Eragrostis pilosa (L.) Beauv. Th
Eragrostis refracta (Muhl.) Scribn. H
Equisetum praealtum Raf.
Erigeron annuus (L.) Pers. Th
Erigeron ramosus (Walt.) BSP. Th
Erythronium americanum Ker. G
Eupatorium album L. H
Eupatorium capillifolium (Lam.) Small H
Eupatorium hyssopifolium L. H
Eupatorium perfoliatum L. H
Euphorbia corollata L. G
Euphorbia nutans Lag. Th

Fimbristylis autumnalis (L.) R. and S. Th
Fragaria virginiana Duchesne H

Galactia regularis (L.) BSP. H

Calax aphylla L. H
Galium aparine L. Th
Galium circaezans Michx. H
Galium pilosum Ait. H
Galium tinctorium L. H
Gaultheria procumbens L. H
Geranium maculatum L. H
Geum canadense Jacq. H
Glyceria striata (Lam.) Hitchc. H
Gnaphalium obtusifolium L. Th.
Gnaphalium purpureum L. H
Goodyera pubescens R. Br. H
Gymnopogon ambiguus (Michx.) BSP. H
Gymnopogon brevifolius Trin. H

Helenium tenuifolium Nutt. Th
Hepatica americana (DC.) Ker. H
Heuchera americana L. H
Hieracium gronovii L. H
Hieracium venosum L. H
Holcus lanatus L. H
Houstonia tenuifolia Nutt. H
Hypericum drummondii (G. and H.) T. and G. Th
Hypericum gentianoides (L.) BSP Th ..... Pineweed
Hypericum mutilum L. H
Hypericum punctatum Lam. H
Hystrix patula Moench. H

Impatiens biflora Walt. Th
Impomoea hederacea Jacq. Th
Ipomoea lacunosa L. Th
Ipomoea pandurata (L.) Mey. G

Juncus effusus L. H
Juncus tenuis Willd. H

Lactuca canadensis L. H
Leersia oryzoides (L.) Sw. H
Leptilon canadense (L.) Britton Th ..... Horseweed
Lespedeza repens (L.) Bart. H
Lespedeza striata (Thunb.) H. and A. H
Lespedeza virginica (L.) Britton H
Liatris graminifolia (Walt.) Willd. G
Linaria canadensis (L.) Dum. Th
Liparis liliifolia (L.) Rich. H
Lobelia cardinalis L. H
Lobelia puberula Michx. H
Luzula carolinae S. Wats. H
Lycopus virginicus L. H
Lygodium palmatum (Bernh.) Sw.

Manfreda virginica (L.) Salisb. G

Mitchella repens L. Ch

Oenothera fruticosa L. H
Onoclea sensibilis L.
Ophioglossum vulgatum L.
Orchis spectabilis L. G
Osmorhiza claytoni (Michx.) Clark H
Oxalis stricta L. H

Panicum anceps Michx. G
Panicum capillare L. Th
Panicum clandestinum L. H
Panicum dichotomum L. H.
Panicum microcarpon Muhl. H
Panicum scoparium Lam. H
Panicum stipitatum Nash H
Paspalum circulare Nash H
Paspalum floridanum Michx. H
Paspalum laeve Michx. H
Passiflora incarnata L. H
Penthorum sedoides L. H
Physalis virginiana Mill. G
Phryma leptostachya L. H
Pilea pumila (L.) Gray Th
Plantago aristata Michx. Th
Plantago lanceolata L. H
Pluchea petiolata Cass. Th
Podophyllum peltatum L. G
Polygala verticillata L. Th
Polygonatum pubescens (Willd.) Pursh G
Polygonum opelousanum Riddell H
Polygonum pennsylvanicum L. Th
Polygonum sagittatum L. Th
Polypodium polypodioides (L.) Hitch.
Polypodium virginianum L.
Polypremum procumbens L. Th
Polystichum acrostichoides (Michx.) Schott.
Potentilla canadensis L. H
Prunella vulgaris L. H
Pycnanthemum flexuosum (Walt.) BSP. H
Pycnanthemum pycnanthemoides (Leavenw.) Fernald H
Pyrola americana Sweet H
Pyrrhopappus carolinianus (Walt.) DC. H

Ranunculus abortivus L. H
Ranunculus hispidus Michx. H
Ranunculus recurvatus Poir. H
Rhexia mariana L. G
Rhynchosia erecta (Walt.) DC. H
Rudbeckia laciniata L. H
Ruellia caroliniensis (Walt.) Steud. G .....Ruellia

Rumex acetosella L. H
Rumex conglomeratus Murr. H
Rumex hastatulus Baldw. H
Rynchospora spp. H (8 spp.)

Salvia lyrata L. H
Sanguinaria canadensis L. G
Sanicula marilandica L. H
Saururus cernuus L. HH
Scirpus atrovirens Muhl. H
Scleria pauciflora Muhl. G
Scutellaria incana Muhl. H
Scutellaria integrifolia L. H
Scutellaria serrata Andr. H
Sedum ternatum Michx. Ch
Senecio aureus L. H
Senecio smallii Britton H.
Seriocarpus asteroides (L.) BSP. H
Seriocarpus linifolius (L.) BSP. H
Setaria geniculata (Lam.) Beauv. H
Setaria lutescens (Weigel.) F. T. Hubb Th
Sida spinosa L. Th
Smilacina racemosa (L.) Desf. G
Solanum carolinense L. G
Solanum nigrum L. Th
Solidago caroliniana (L.) BSP. H
Solidago juncea Ait. H
Solidago nemoralis Ait. H
Sorghastrum nutans (L.) Nash H
Specularia perfoliata (L.) A. DC. Th
Sporobolus poirettii (R. and S.) Hitchc. H
Stenophyllus capillaris (L.) Britton Th
Strophostyles umbellata (Muhl.) Britton G
Stylosanthes biflora (L.) BSP. H

Talinum teretifolium Pursh H
Taraxacum officinale Weber H
Tephrosia virginiana (L.) Pers. H
Tiarella cordifolia L. H
Tipularia discolor (Pursh) Nutt. G
Tragia nepetaefolia Cav. H
Trichostema dichotomum L. Th
Trillium catesbaei Ell. G
Triodia flava (L.) Smyth H
Typha latifolia L. HH

Uvularia sessilifolia L. G
Uvularia perfoliata L. G

Verbena urticaefolia L. H
Verbesina occidentalis (L.) Walt. H
Vernonia noveboracensis (L.) Willd. H

Viola spp. H (15 spp.) Th (15 spp.) ..... Violet

Waldsteinia doniana Tratt. H.
Woodsia obtusa (Spreng.) Torr.

Xanthium canadense Mill. Th
Xanthium echinatum Murr. Th

Zanthorhiza apiifolia L'Her. N
Zephyranthes atamasco (L.) Herb. G ..... Atamasco lily
Zizia aurea (L.) Koch H

The Taxonomy and Cytology of Saxifraga pensylvanica L. and Related Forms*

George W. Burns

Introduction

Saxifraga pensylvanica[1] was founded in 1753 by Linnaeus (6) who described its range as "Virginia, Pensylvania, and Canada." Material from eastern United States appeared uniform at first and presented no particular problem. However, with later collection, especially in the western part of the range, a rather large amount of variation[1a] has been met with, and it became apparent that *S. pensylvanica* L. constitutes a polymorphic species. It is with the basis of this polymorphism and its effect on the taxonomy of the species, that the present study is concerned.

Early practice in dealing with newly found variants of *S. pensylvanica* appears to have been simply the broadening of the original description of the species. For example, leaves have been variously described as "broadly lanceolate" (Don [2]), "oblanceolate or oval" (Torrey and Gray [13]), "narrowly oblong or elliptic to spatulate" (Small and Rydberg [10]), "sub-linear to oblong, glabrous to hirsute" (Engler and Irmscher [4]), or "oblong-spatulate" (Engler [3]). Floral parts are similarly treated. The taxonomic limits of *S. pensylvanica* became further confused in 1870 with the description of a new, but morphologically similar species, *S. Forbesii Vasey*, from shaded cliffs in southern Illinois.[2] Material from similar habitats in central Missouri was then indiscriminately labeled either *S. Forbesii* or *S. pensylvanica*. Later workers have variously reduced *S. Forbesii* to a synonym of *S. pensylvanica*, or a variety of the latter, while others have restored it to specific rank.

A number of workers have attempted revision of the taxonomic limits of *S. pensylvanica*, setting up various subdivisions of it in some cases, or segregating certain variants into new species, or even considering the whole range of variation as a single, unified species. Johnson (5) in 1923 published his revision of the section *Boraphila* of the genus *Saxifraga*, in which he recog-

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* A thesis submitted to the Graduate Faculty of the University of Minnesota in partial fulfillment of the requirements for the degree of Doctor of Philosophy, December, 1941.

1 Although the adjective *pennsylvanicus, -a, -um* has been in general use since the time of Torrey, the original Linnaean spelling with a single *n* is retained here. *Vid.* Fernald, 1940, "*Pensylvanicus* or *pennsylvanicus*?" Rhodora **42**: 94-5.

1*a* Particularly in the size and shape relations of follicles, petals and leaves, in inflorescence pattern, and habitat.

2 Type locality, Makanda, Ill.

nized some of the morphological variants of *S. pensylvanica*, establishing three segregates from it as new species. He also raised *S. Forbesii* from a variety of *S. pensylvanica* (which disposition had been made in *Das Pflanzenreich*) to a separate species. In 1928, Bush (1) published a revision of a number of species of *Saxifraga*, among them *S. pensylvanica* and the new species of Johnson's. These latter Bush reduced to varietal rank under *S. pensylvanica* on the basis of their being "probably mere variations." However, he established three new varieties of his own. The disposition of these and other treatments is taken up in the systematic section of the present paper.

The status of *S. pensylvanica* was by this time thoroughly confused. It was recognized that a considerable amount of variation occurred in the species, but previous workers had handled the situation on purely subjective grounds, each in a slightly different way. There appears to have been no attempt to reduce the variation to concrete, quantitative bases, or to establish the cause for it. The range of variation in size and shape relations of vegetative and floral parts, color differences, occurrences of such other distinctive characters as foliaceous inflorescence bracts, or of variation in inflorescence habit suggest a number of contributing causes. Differences in size and shape relations of parts strongly suggest polyploidy, occurrences of foliaceous bracts might be correlated with gene action, and differences of inflorescence pattern were perhaps to be associated with gene action or might be environmentally induced, hence non-heritable. Accordingly, the problem here has been first, to test the possibility of establishing the thesis that variation in *S. pensylvanica* is not random, but orderly; that it is in part heritable, and in part non-heritable; that it is the visible effect of three forces acting on the phenotype, i.e., polyploidy, genic modification, and environmental influence; and second, to formulate a natural classification of *S. pensylvanica* and related forms based upon those findings.

Approach to the problem has been along several lines. Field study was made by the author to determine first-hand the range of variation[3] and to attempt a classification of it. Collections of living material were made from as many different localities and habitats as possible, and the specimens so collected grown in greenhouses and coldframes under similar conditions of light, water, and temperature in order to test the magnitude of the effect of environment on form, and to supplement seasonal morphological observations in the field. Such studies on living material and the author's own collection of dried specimens were extended by the examination of herbarium material from a number of sources. Morphological studies were expanded to include an attempt to reduce certain obvious differences to a quantitative basis; a beginning along this line has been made with variation in leaf shape of polyploids.[4] In the line of cytological study, the attempt has been to correlate the major subdivisions of the variation pattern in *S. pensylvanica* with polyploidy.

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3 Minnesota material is particularly good in this respect since all but the purple flowered form occur within its borders.

4 *Vid.* pp. 134-135.

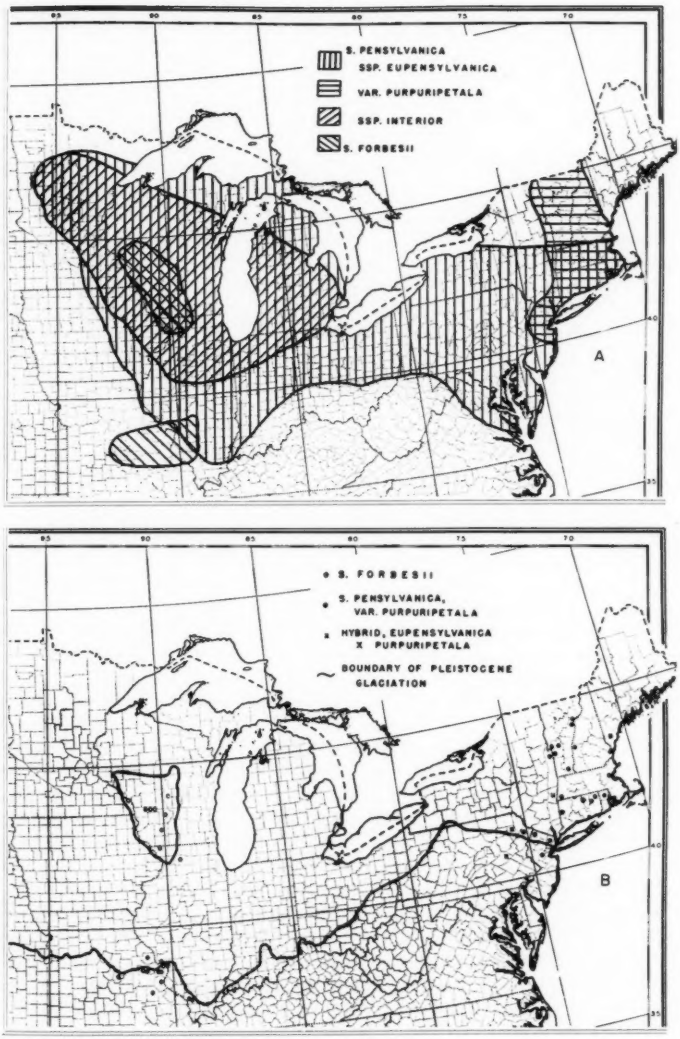

Fig. 1. Distribution maps of *S. pensylvanica* and *S. Forbesii*. A. Generalized range map; B. distribution map showing locations for specimens examined. Note relation of *S. Forbesii* to glaciation.

Material and Methods

Morphological studies here have been based on examination of both living and dried specimens. The former have been observed both in the field in as many different localities and habitats as possible, and in cultivation under controlled conditions with plants obtained from a number of sections of the range.[5] Dried specimens were made of plants collected by the author in the western part of the range, and use was made of all the material from the following herbaria: The University of Minnesota, the United States National Museum, the Missouri Botanical Garden, the University of Illinois, the University of Wisconsin, and the University of Pennsylvania.

Chromosome studies were made from both sporogenous and somatic material. For the former, entire cymules, rather than individual buds, were employed because of the small size of buds and anthers at microsporogenesis. Both Navashin (Belling's modification) and La Cour's 2BE were found to give good results in cytological studies. Crystal violet was used with success, but required two stages of mordants: one-half to two hours in 2% aqueous chromic acid before the stain, and one minute in 2% IKI in 85% ethyl alcohol just prior to final dehydration after staining. Slides were usually left in the stain 6-12 hours to avoid rapid and uncontrollable destaining in the final stage of absolute alcohol. Clarite in toluene was used as a mounting medium to prevent fading of the stain.

Because of the relatively high number of chromosomes and their broad vertical distribution in both sporocytes and root tip cells, it was not possible to focus on the entire complement at one time under oil immersion, making necessary the use of camera lucida drawings, rather than photomicrographs, both for initial counts and for final records. Such drawings were prepared with the aid of a Spencer camera lucida at a table magnification of x2800.

Records of size differences of leaf epidermal cells of the various polyploid forms were also made by camera lucida, at a table magnification of x300. Both living and dried specimens were drawn upon in this study, corresponding parts of mature leaves being punched out for use in both cases. Living material was fixed 24-48 hours in Conant's FAA and sectioned at 10 micra. Tannic acid and ferric chloride was found to give most satisfactory staining results in such instances. In the case of dried specimens, drawings were made from whole-mounts which had been cleared either in Conant's FAA at room temperature for 48 hours, or in a mixture of 95% alcohol and chloral hydrate at boiling temperature for a few hours. Comparison of material from a leaf treated in each of the two latter ways showed no appreciable differences in cell size or shape. In this study, cell surface area was obtained from the camera lucida drawings by means of a planimeter, and converted to square micra for comparison of the various polyploid forms.

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5 For range, see Fig. 1a.

Cytological Aspects of the Group

By and large, polymorphism in *S. pensylvanica* has come about in three principal ways: (1) formation of distinctive intraspecific chromosome races through autopolyploidy; (2) hybridization bewteen and within the intraspecific chromosome races; and (3) genic differentiation within such races.

The gametic chromosome number 28[6] was determined early in the present study for material of *S. pensylvanica* which most nearly coresponds to the original Linnaean concept[7] (ssp. *eupensylvanica*, ssp. nov.). The same number was similarly found to obtain in the purple flowered form of *S. pensylvanica* and in *S. Forbesii*. The gigas characters of what Johnson (5) had designated *S. crassicarpa*, however, strongly suggested polyploidy, and subsequent cytological examination disclosed the gametic chromosome number to be 56 (octoploid). Inasmuch as certain morphologically distinctive chromosomes were observed to occur in the doubled number, it is evident that this form is an autopolypolid. Such observations could not be extended to the entire complement with any degree of certainty because of the essential similarity of many of the chromosomes. Moreover, no other potential parent exists within the range of the octoploid entities, so that allopolyploidy may be ruled out.

Where tetraploid and octoploid forms of *Saxifraga* occur together, it is logical to expect a hexaploid also, in view of the general ease with which all members of the genus exchange genes and hybridize. Accordingly, a new and puzzling form, occurring in mixed growth of 4n and 8n plants, differing from both but exhibiting certain intermediate characters, suggested a possible hexaploid hybrid. Examination of root tip material disclosed the expected 6n chromosome complement (Fig. 2e). While artificial reproduction of this form from a cross between the tetraploid and octoploid will be necessary before its hybrid origin can be substantiated, it seems reasonable to so postulate at this time. The follicles of the 6n form are long and relatively slender, superficially suggesting those of the 4n plants, but generally somewhat less divergent (like the octoploids), long tapering after the manner of the tetraploids, but, like the octoploids, with style short or obsolescent. Filaments and petals are longer and narrower than the tetraploids, but the sepals strongly suggest those of the 8n group. Unlike either of its probable parents, the nectary persists in fruit as a prominent ridge surrounding the lower middle of the carpels, and inferiority of the ovary is much more pronounced. These last characteristics, however, would appear more apparent than real. Inasmuch as fertility is low and erratic, development of the pistil remains in a semi-juvenile stage as regards inferiority and the location of the persistent nectary, the fruits at maximum development resembling earlier stages of the 4n and 8n forms. In any event, however, such increased inferiority of the ovary is taxonomically reliable here.

That hybridization may and does occur within as well as between intra-

[6] Here considered tetraploid, since the basic number for the genus is set at n = 14; see p. 135.

[7] For the basis of the interpretation of the Linnaean type, see p. 144.

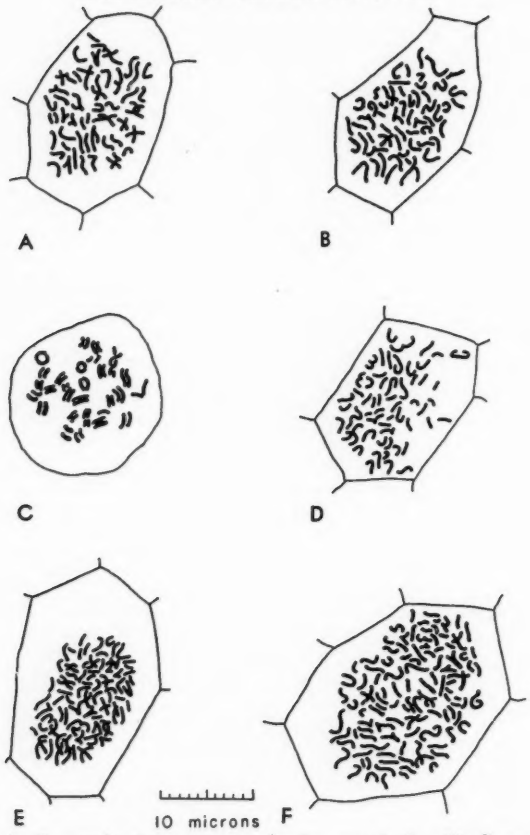

Fig. 2. A. *S. pensylvanica*, ssp. *eupensylvanica*, root tip 2n=56; B. var. *purpuripetala*, root tip 2n = 56; C. *S. Forbesii*, microsporocyte at synapsis n = 28; D. *S. Forbesii*, root tip 2n = 56; E. *S. pensylvanica* ssp. *tenuirostrata*, root tip 2n = 84; F. ssp. *interior*, var. *crassicarpa*, root tip 2n = 112.

specific chromosome races in *S. pensylvanica* is evident in the occurrence of a hybrid swarm between *S. pensylvanica*, ssp. *eupensylvanica* and its variety *purpuripetala* in Delaware and eastern Pennsylvania and New York, in the area of overlap of the ranges of these two entities. The hybrid nature of this form is evident in the greenish-white petals which are streaked and otherwise mottled with purple, the filaments which may be colorless or purple, the leaves which have only a few coarse hairs,[8] and in the morphology of the follicles

[8] Leaves of ssp. *eupensylvanica* are variously hirsute or tomentose; those of var. *purpuripetala* are leathery and glabrous.

and other floral parts. It is probable also that other hybrid swarms within *S. pensylvanica* will be turned up wherever ranges of distinctive and stable variants overlap.

The effect of genic influence on phenotype, third of the factors underlying polymorphism in *S. pensylvanica,* is evident in both the tetraploid and octoploid races. While cyto-genetic investigations would have to be made to verify the assumption of genic influence here, such assumption at the present time would seem to be the only logical one to account for constant differences of phenotype within intraspecific chromosome races. In the tetraploids, this influence finds expression in both morphological and physiological characters, the first of these in size and shape relations of floral parts, and the latter in color of parts at least, and in ecological requirements as well, if *S. Forbesii* is considered. In the ocotploids, genic variation would appear to be responsible for difference of inflorescence pattern, leaf shape, and size and shape relations of floral parts. It is assumed that phenotypic differences in a number of characters are due to action of several genes. In both tetraploids and octoploids, forms differing only in a single characteristic (*i.e.,* possession of foliaceous inflorescence bracts) are assumed to be correlated with single gene action. No variants of the hexaploid are known.

Where a little is known about the inter-relations of a group, it is tempting to speculate on the origin of certain probably derived forms. Here it seems likely that var. *purpuripetala* has been derived from ssp. *eupensylvanica* by simple genic differentiation alone, and that recently, since it occupies the same sort of habitat as ssp. *eupensylvanica,* in the northeastern extreme of the range. The case for *S. Forbesii,* however, presents some difficulties. If it has been derived from ssp. *eupensylvanica* in the same way as that postulated for var. *purpuripetala,* such derivation is probably considerably older, as the discontinuous range of *S. Forbesii* would indicate (Fig. 1a, b). In any event, it is probable that in this instance genic influence, in addition to the obvious morphological peculiarities, is expressed in a specificity of ecologic requirement not occurring in the *S. pensylvanica* complex. *S. Forbesii,* so far as known, occurs only on moist, shaded sandstone or quartzite cliffs, while the *pensylvanica* complex is found wherever sufficient moisture is present, in sun or shade, throughout the range. In the octoploids, on the other hand, the morphologic characteristics of var. *congesta* (p. 155) suggest two possible explanations. It may be either a genic modification, or possibly a polyploid of longer standing which has progressed along a line of phenotypic reversion to something approaching the general habit of the tetraploid.[9]

A number of morphologic characteristics are correlated with polyploidy in *S. pensylvanica;* these include: gigas characters (var. *crassicarpa*); stoutness of scape (var. *crassicarpa*); shorter and broader leaves and floral parts (vars. *crassicarpa* and *congesta*); larger seeds, shorter and broader follicles, and increased cell size (vars. *crassicarpa, congesta* and *winnebagoensis*). This is in substantial agreement with other work of the same sort which has been reviewed by Müntzing (7).

9 As suggested by Wettstein (14).

The matters of reduced length-width ratio in polyploid leaves and of increased cell size have been treated quantitatively in the present study. Early in the investigation it was noted that most of the leaves of herbarium spcimens of the 4n and 8n plants differed markedly in shape. The same difference was

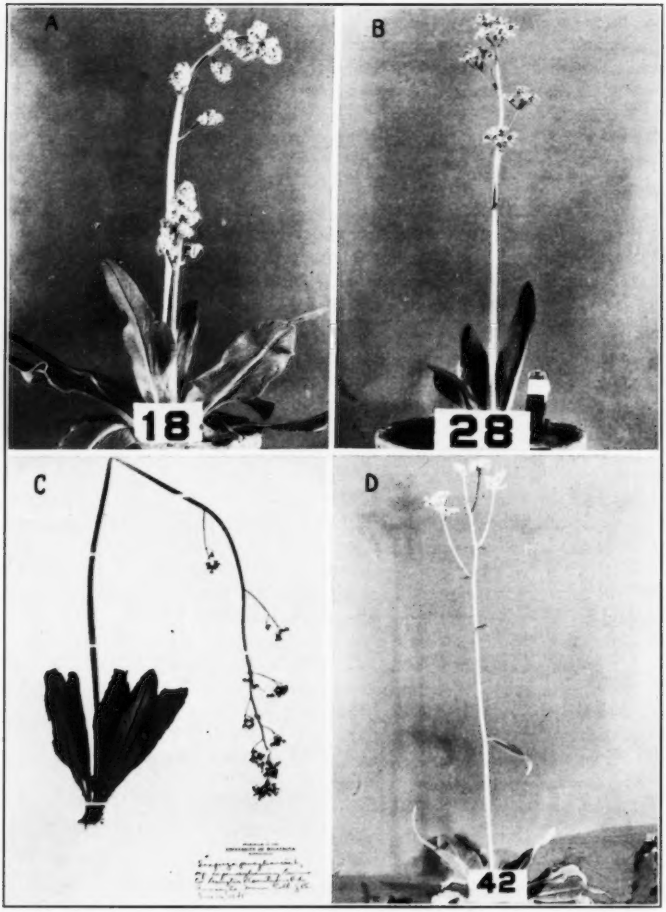

Fig. 3. A, B. *S. pensylvanica*, ssp. *eupensylvanica*. Effect of shade on inflorescence pattern; both plants collected from open meadow, and having same inflorescence form when collected. Plant 28 grown one year in shade; no. 18 kept in sun; C. ssp. *eupensylvanica*; D. *S. Forbesii*, f. *bracteosa*.

evident in the field (Figs. 3, 4), the leaves of the 8n plants appearing noticeably wider for their length than those of the 4n plants. Accordingly, mature leaves of 50 plants, selected at random, were measured for length-width ratios. Leaves of the 4n plants were found to be 4.67 ± 1.109 times as long as wide, and those of the octoploids $3.44 \pm .837$ times longer than wide. Application of the standard deviations to the means gives a range of 3.561-5.779:1 for length-width ratio of tetraploid leaves, and 2.603-4.277:1 for octoploids. This overlapping of the ranges reflects an actual situation, for a few octoploid leaves are quite similar to those of the tetraploids. Statistical tests show the probability of the difference between the two sample means being due to errors of sampling to be far less than one in 10,000, and the difference is here considered significant.[10]

That these geometric changes are due to increase in cell size, rather than in cell number, is indicated by a study of lower leaf epidermal cells (Figs. 5, 6, 7). Measurements of approximately 200 cells each for the 4n and 8n plants, selected at random, gave a range of means for individual tetraploids of 1147-1897 square micra, and for octoploids, 2294-3408 square micra.[11] These ranges were established from plants where the chromosome number had actually been counted previously. In each case, larger cell size, subglobose follicles and 8n chromosome number were correlated, and in each of the plants at least some of the leaves showed a reduced length-width ratio. In view of this consistent relationship, it is felt that careful areal measurements of leaf epidermal cells in *Saxifraga pensylvanica* will serve to indicate to which chromosome race any puzzling forms might belong. A number of such forms were so measured, including those of vars. *crassicarpa*, *congesta*, and *winnebagoensis*, and were found to fit into the previously established ranges for known tetraploids and octoploids.

While a single basic chromosome number for the *Saxifragaceae* is difficult to designate in the light of the present knowledge of the family (gametic numbers 6, 7, 8, 9, 10 and euploid series thereof are reported for various members of the family in its broadest sense), it appears likely that 14 is the basic number for the genus *Saxifraga*. So far as is known, it is possible to derive all numbers in the genus from 14, and Schoennagel (8), in his extensive review of the *Saxifragaceae*, feels that 14 is basic for *Saxifraga*. The only report in the literature on chromosome number for any of the saxifrages which have formed a part of this study appears to be one by Skovsted (9) for *S. pensylvanica* as $n=29$. The relation of such an anomalous number to the 14-series is not altogether clear, and careful investigation has consistently demonstrated the gametic number for *S. pensylvanica*, ssp. *eupensylvanica*, and its var. *purpuripetala*, as well as *S. Forbesii*, to be 28 rather than 29. Accordingly, the position of these three entities as tetraploids becomes clear, and their relation, as well as of their hexaploid and octoploid derivatives, to the genus is logical.

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10 Standard error of the difference of the means, .193876.

11 Averages of the means are as follows: 4n, 1608 square micra; 8n, 2739 square micra.

The Systematics of the Group

On the basis of cytological data which indicate a high degree of polyploidy and hybridization, correlated with morphological distinctions, *S. pensylvanica* is here regarded as a polymorphic species, subdivided into several sub-categories on the basis of what are felt to be natural relationships. These taxonomic categories, and the criteria for their use here, are:

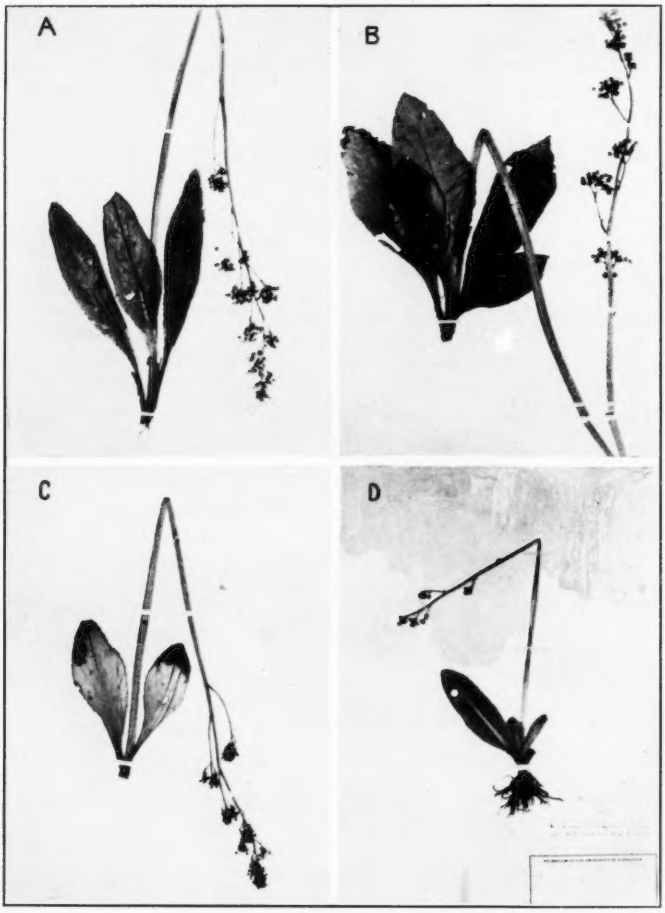

Fig. 4. A. *S. pensylvanica*, ssp. *tenuirostrata*; B-D. ssp. *interior*: B. var. *crassicarpa*; C. var. *congesta*; D. var. *winnebagoensis*.

a. *form:* those entities differing from the type in the expression of a single morphological character (single gene action), and which have no distinct range;

b. *variety:* those entities differing from the type in the expression of several morphological and/or physiological characters (which may be most logically assumed to be due to the effect of multiple factors because of the number and diversity of such characters, but which might possibly be related to pleiotropic effect of single genes, or multiple alleles), and which have or probably have a distinct range;

c. *subspecies:* those entities differing from the type in several morphological characters and also in chromosome number, but which are connected to the type by intergrading individuals, and which have, or will probably prove to have, a distinct range.

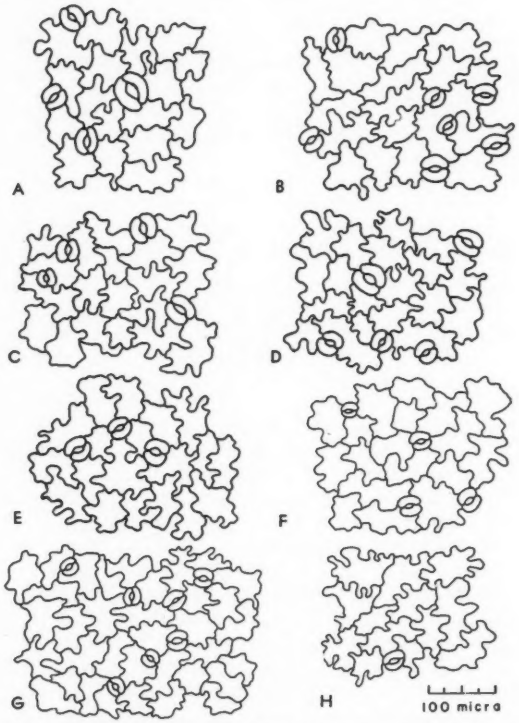

Fig. 5. Epidermal cells from tetraploid leaves. Average areas in square micra (except as noted, figures are from ssp. *eupensylvanica*): A. 1479; B. 1147; C. 1649; D. 1455; E. 1822; F. (var. *purpuripetala*) 1819; G. 1255; H. *(S. Forbesii)* 1897. Compare with Figs. 6 and 7.

Where differences are of major magnitude, and there are no intergrading forms, specific rank is assigned.

It is felt that the various subdivisions of *S. pensylvanica* which have been recognized on the basis of inflorescence pattern or pubescence of leaves or scape are without taxonomic significance. These include first, vars. *α conglomerata* Ser., a form "with dense panicles, flowers conglomerate" (Seringe in DC. Prodromus *IV:* 39), and *β corymbifera* with "lax panicles, flowers distant, corymbose" (Seringe, *op. cit.*). Michaux, in the *Flora Boreali Americana,* notes these variations, which were maintained by Torrey and Gray (13). Johnson (5), in his revision, speaks of these variations but makes no disposition of them. It has been found in the present study, however, that these represent merely sun and shade forms, respectively, and furthermore can be distinguished only in the later stages of flowering. Examination of herbarium specimens has revealed, in every case where habitat notes appear on the label, that plants answering to the description of *α conglomerata* were collected in open, sunny situations. On the other hand, those of the *β corymbifera* type are from shaded localities, chiefly swampy woods. Moreover, collection and field study by the author has revealed only the loose, open inflorescence in woods, and the conglomerate forms in open meadow habitats. The total lack of value of inflorescence pattern here as a taxonomic character, however, is conclusively demonstrated by the fact that plants of shaded habitats produce the inflorescence of the sunny habitat when grown in full sun in cultivation, and that plants collected from open meadows produce the inflorescence of shaded habitats when grown in shade in the greenhouses (Fig. 3a, b).

On the basis of leaf pubescence, Sternberg (11, 12) recognized three forms, which are here held to be taxonomically invalid: f. 1. *Linnaei,* "leaves hirsute on both sides"; f. 2. *Haworthii,* "leaves glabrous above, hirsute below"; f. 3. *glabra,* "leaves glabrous on both sides." Except for var. *purpuripetala,* no forms corresponding to "f. 3. *glabra*" have been encountered in the present investigation. It is not possible to determine whether Sternberg had reference to the whitish- or to the purple-flowered form, though the former is suspected since no difference other than those of lack of pubescence are cited. In the rest of the *S. pensylvanica* group, variation in amount and location of pubescence does occur, but the plants are morphologically indistinguishable otherwise, both in vegetative and in floral parts. Since the only diagnostic character is the variable one of pubescence, it is felt that these forms of Sternberg should not be recognized.

Johnson (5) in 1923 distinguished several of the variants of *S. pensylvanica* as new species, as pointed out earlier in the present paper. These new species included *S. crassicarpa,* distinguished by the "stout, globose and thick-beaked" follicles, larger seeds and "few-flowered, coarse inflorescence"; *S. purpuripetala,* distinctive because of (purple) "colored petals and peculiarities of carpels, gland, seeds and habit"; and *S. winnebagoensis,* segregated on the basis of "unusually small follicles and rather leathery, yellowish-tinged leaves." The limits of *S. pensylvanica* itself and of *S. Forbesii* as understood by Johnson were not given. *S. crassicarpa* has been shown, by chromosome counts and

cell size studies, to be octoploid; *S. winnebagoensis* has also been assigned to the octoploid complex. In the latter case, although no living material, or viable seeds for germination, were available so that chromosome counts could be made, measurements of cell size confirmed the preliminary conclusion, on morphological grounds, that *S. winnebagoensis* belonged with the octoploids. *S. purpuripetala,* tetraploid, has, on the bases of morphology and range, been given varietal rank under ssp. *eupensylvanica. S. Forbesii* is held to be a distinct species. For a full account of the bases for disposition of each form, see their descriptions pp. 151 to 156.

Bush (1) in 1928 revised *S. pensylvanica* still further, reducing Johnson's species to varieties on the basis of their being "probably mere variations," but he set up three new varieties of his own because of apparent differences of inflorescence pattern and pubescence. These included vars. *hirsuta, tomentosa,* and *dichotoma. S. Forbesii* was again reduced to varietal status under *S. pensylvanica,* Bush assigning the name "*S. pennsylvanica* L., var. *Forbesii* (Vasey)

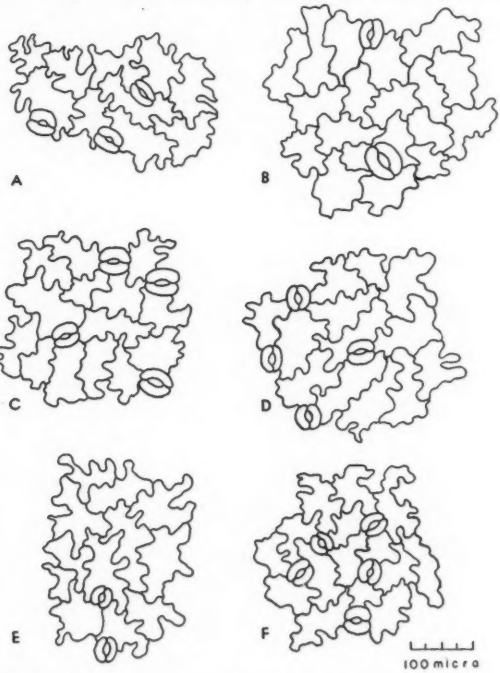

Fig. 6. Epidermal cells from octoploid leaves (ssp. *interior*, var. *crassicarpa*), with average areas in square micra: A. 3125; B. 3050; C. 2749; D. 3408; E. 2378; F. 2513.

Bush" to it, a later homonym inasmuch as Engler and Irmscher had made the same disposition in *Das Pflanzenreich* in 1916.

Examination of the first two of these varieties, *hirsuta* and *tomentosa*, reveals nothing distinctive about them, except the location of more abundant pubescence, and therefore, it is felt, these varieties should be discarded. Apparently, though, Bush has included in his variety *dichotoma* several different sorts of things. Examination of the specimens in the University of Minnesota herbarium from Gwinn's Bluff, Winona Co., Minnesota, which he cites, together with collections by the author at the spot, indicate that these are *S. Forbesii*. In the cited specimens, follicles and flower parts are clearly those of *S. Forbesii*, and the habitat is moist, shaded sandstone cliffs. Other specimens cited by Bush are, in part, the octoploid form (var. *crassicarpa*) and partly straight tetraploid (ssp. *eupensylvanica*) so far as morphological study reveals. Since these varieties are founded on the variable and unreliable character of pubescence which is not correlated with any other distinction, or an environmental

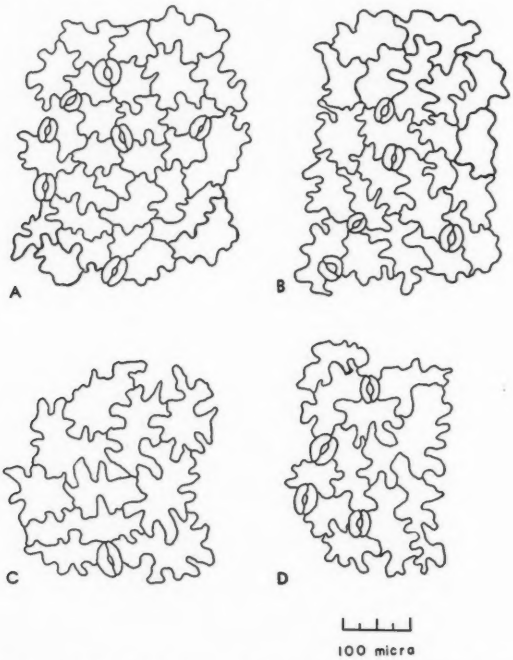

Fig. 7. Epidermal cells from leaves of various polyploid forms, with average areas in square micra: A. ssp. *interior*, var. *winnebagoensis* (2340); B. ssp. *interior*, var. *crassicarpa* (2990); C. ssp. *tenuirostrata* (4903); D. ssp. *interior*, var. *congesta* (3141).

modification spread through several taxonomic entities, their maintainance here is unsound and without purpose.

In place of the subjective treatments based on characters of little or no taxonomic value, a classification is here proposed on the basis of cytology and morphology, which may be keyed as follows:

I. Follicles erect throughout most of their length, the tips usually divergent; the styles various, erect to recurved; plants of bogs and wet meadows. *S. pensylvanica* group.

A. Petals narrowly lanceolate, 1-nerved, greenish-white or purple; styles mostly over 1 mm. long; follicles inflated only below; leaves mostly lanceolate, or occasionally lance-ovate.

1. Follicles appearing essentially superior at maturity, the nectary forming an obsolescent, scarcely visible ridge around them just above the point of their adnation to the hypanthium; upper part of follicles rather stout and abruptly tapering, never erect at the tip.

a. Petals greenish-white, leaves variously hirsute.

1. Bracts linear, .5-2.5 cm. long. ..... 1. *S. pensylvanica*, ssp. *eupensylvanica*.

2. Bracts oval, 7-10 cm. long. ..... 2. *S. pensylvanica*, ssp. *eupensylvanica*, f. *fultior*.

b. Petals purple; leaves dark, leathery, glabrous.

1. Bracts linear, less than 2 cm long. ..... 3. *S. pensylvanica*, ssp. *eupensylvanica*, var. *purpuripetala*.

2. Bracts lanceolate to ovate, 2-5 cm. long. ..... 4. *S. pensylvanica*, ssp. *eupensylvanica*, var. *purpuripetala*, f. *bracteatis*.

2. Follicles 1/3 to 1/2 inferior at maturity, the nectary forming a prominent swelling around them just above the point of their adnation to the hypanthium; upper part of the follicles slender and long-tapering; erect or divergent at the tip. ..... 5. *S. pensylvanica*, ssp. *tenuirostrata*.

B. Petals mostly ovate to lance-ovate, 3-nerved, greenish-white, rarely white; styles mostly less than 1 mm. long; follicles sub-globose, inflated throughout their length; leaves mostly ovate to obovate.

1. Follicles large, 4-5 mm. long, 3-4 mm. wide; styles over .5 mm. long in fruiting stages.

a. Bracts linear, to 2 cm. long. ..... 6. *S. pensylvanica*, ssp. *interior*, var. *crassicarpa*.

b. Bracts ovate, 2.5-7 cm. long. ..... 7. *S. pensylvanica*, ssp. *interior*, var. *crassicarpa*, f. *bracteata*.

2. Follicles smaller, about 2 mm. long, 1-1.5 mm. wide; styles .5 mm. or less in length in fruiting stages.

a. Flowers numerous, in congested, conglomerate cymules; styles present, to .5 mm long, more or less divergent; inflorescence never spicate; leaves obovate, crenulate, dark green. 8. *S. pensylvanica*, ssp. *interior*, var. *congesta*.

b. Flowers fewer, borne in open cymules; inflorescence more or less spicate; syles shorter than .25 mm. or entirely absent, the more or less sessile stigmas on the summits of the follicles; leaves lanceolate, yellowish-green, entire or occasionally somewhat denticulate. ..... 9. *S. pensylvanica*, ssp. *interior*, var. *winnebagoensis*.

II. Follicles divergent throughout most of their length; styles always recurved; plants of moist, shaded, chiefly sandstone cliffs. ..... *S. Forbesii* group.

A. Bracts linear, to 1.5 cm. long. ..... 10. *S. Forbesii*.

B. Bracts lance-ovate, to 9 cm. long. ..... 11. *S. Forbesii*, f. *bracteosa*.

I. SAXIFRAGA PENSYLVANICA L., species polymorpha.

Michx., Fl. Bor. Am. *I:* 269, 1803. Bieglow, Fl. Boston., 107, 1814. Don, Trans. Linn. Soc., **13**: 384, 1822. De Candolle, Prodromus *IV:* 39. 1830. Engler, Monogr. Gatt. Sax., 149, 1872. Britton and Brown, Ill. Fl. No. U. S., *II:* 173, 1897. Small, N. A. Fl. **22**(2): 139, 1905. Robinson and Fernald, Gray's New Man. Bot., ed. 7, 446, 1908. Engler and Irscher, Pflanzenreich *IV*(117): 65, 1916.

Syn.: ?*S. semipubescens* Sweet, Hort. suburb. 97. 1818.
Micranthes pennsylvanica (L.) Haw., Enum. Sax. 45. 1821.
M. hirta Haw., Enum. Sax. 46. 1821.
S. hieracifolia Haw., Enum. Sax. 45, non L., 1821.
S. palustris Link., Enum. hort. Berol. *I:* 412. 1821.
?*S. semipubescens* D. Don, Trans. Linn. Soc. **13**: 385. 1822.
S. noveboracensis Cold., Noveb. 105.
S. pensylvanica L., *α conglomerata* Ser., and *β corymbifera* Ser., DC. Prodr. *IV:* 39. 1830.
S. marilandica Hort. ex. Ser., Ser. in DC Prodr. *IV:* 39. 1830.
S. pennsylvanica L., f. 1. *Linnaei* Sternb., Rev. Saxifrag., Suppl. II: 44. 1831; f. 2. *Haworthii* Sternb., loc. cit.; f. 3. *glabra* Sternb. *loc. cit.*
Euaeizoa pennsylvanica (L.) Raf., Fl. Tell. *II:* 71. 1836.
S. pennsylvanica L., var. *typica* Engl. & Irm., Pflanzenreich *IV*(117):65. 1916.
S. pennsylvanica L., var. *hirsuta* Bush, Amer. Midl. Nat. **11**: 230. 1928; var. *tomentosa* Bush, Amer. Midl. Nat. **11**: 231. 1928; var. *dichotoma* Bush, in part, Amer. Midl. Nat. **11**: 232. 1928.

Leaves to 3 dm. long, lanceolate, ovate or obovate; glabrous or, when pubescent, the hairs not arising from prominent, minute papillae; entire to denticulate. Inflorescence cymose-paniculate or spicate; bracts linear or foliaceous; cymules congested and conglomerate, or open; few or many flowered. Petals linear to ovate, 1-3-nerved, white, greenish-white, purple, or whitish mottled with purple; follicles divergent only at the extreme tip, or not at all; styles to 1.5 mm. long or absent, erect or recurved. Plants of bogs and wet meadows.

1. **S. pensylvanica** L., ssp. **eupensylvanica** ssp. nov.

Dill., Hort. Elth. 1732. Linn., Sp. Pl. 399, 1753. Linn., Sp. Pl. *II*, **1**: 640, 1799. Sternb., Rev. Saxifrag., 8, 1810. Pursh, Fl. Amer. Septentr. *I:* 311, 1814. Torrey and Gray, Fl. N. A. *I:* 571, 1838-40.

Syn.: *S. pensylvanica* L., Sp. Pl. 399, 1753.
?*S. semipubescens* Sweet, Hort. suburb. 97. 1818.
S. pennsylvanica L., var. *hirsuta* Bush, in part, Amer. Midl. Nat. **11**: 230. 1928; var. *tomentosa* Bush, in part, Amer. Midl. Nat. **11**: 231. 1928; var. *dichotoma* Bush, in part, Amer. Midl. Nat. **11**: 232. 1928.

Folia basalia ad 3 dm. longa, plus minusve anguste lanceolata, integra vel denticulata, supra vel infra vel utrinque hirsuta; caulis floriferus 3-11 dm. altus, ramis primariis inflorescentiae adscendentibus, 2-10 cm. longis; cymulis apricis congestis vel umbrosis apertis; sepala deltoidea, 1.5-2.0 mm. longa, 1.5-2.0 mm. lata, trinervata; petala plerumque subviridia, rare alba, linearilanceolata, 3-4 mm. longa, .5-7 mm. lata, uninervata; ovaria 1/5-1/4 inferia; carpella follicularia, tantum superioria in fructu, 2 mm. longa, 1.5 mm. lata, gracilia, erecta vel parce divergentia; semina fusca, tuberculata, unilateraliter carinata, 1.0 mm. longa, .35 mm lata. *S. pensylvanica* L. sensu strictiore.

Leaves in a basal rosette, to 3 dm. long, persisting over winter; more or less narrowly lanceolate, length-width ratio about 4.7:1; entire to distantly denticulate; tapering below to a margined petiole, 1-10 cm. long; blades variably hirsute, above or below, or both; the hairs subulate, lax, 1-2 mm. long.

Inflorescence cymose-paniculate, scape 3-11 dm. high, glandular-pilose, often densely so, bearing divergent or ascending branches 2-10 cm. long in the

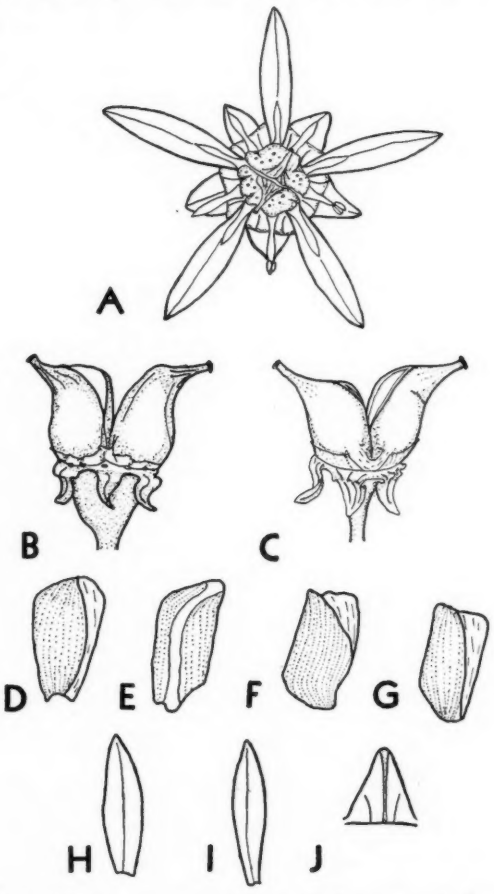

Fig. 8. *S. pensylvanica*, ssp. *eupensylvanica*. A. flower at anthesis (×5); B, C. mature follicles (×5); D-G. seeds (×20); H, I. petals (×5); H, I. petals (×5); J. sepal (×5).

axils of linear, entire to denticulate bracts 5-25 mm. long. Inflorescence compact in sun habitats and branches shorter, becoming lax and open in shade.

Sepals green, deltoid, acute or occasionally obtuse, slightly united at the base, 1.5-2 mm. long, 1.5-2 mm. wide, 3-nerved, the 2 laterals disappearing short of the apex, the midvein continuous to the apex where it forms a dark tip; reflexed at anthesis, becoming reflexed-appressed in fruit; petals mostly greenish-white, rarely white, lance-linear, acute, 3-4 mm. long, .5-.7 mm. wide, 1-nerved with a prominent costa; filaments white to pale brownish, subulate, acute, slightly narrowed 1/3 above the base, the anthers reddish-orange. Hypanthium adnate to the bi-carpellate ovary 1/5 - 1/4 above the base; ovary depressed in early anthesis and enclosed by a verrucose, slightly rugose, greenish-yellow nectary; the carpels becoming elevated in fruit above the gland, which persists as an obsolescent ridge around the carpels less than 1 mm. above the point of their adnation to the hypanthium. Carpels united at the bases only, follicular in fruit, appearing essentially superior at maturity, about 2 mm. long and 1.5 mm. wide; slender, erect or slightly divergent at the tips, dilated below but tapering gradually above to a slender, obscurely veined style. Styles 1.0-1.5 mm. long, divergent 45°-90°, stigmas small, only slightly expanded. Seeds brown, with a constriction at each end, tuberculate, carinate along one side, 1.0 mm. long, .35 mm. wide (Figs. 3, 8).

Chromosome number: n=28! (Fig. 2).

Habitat: bogs and wet meadows.

Distribution in U. S.: Mass. to cen. Va., w. along Great Lakes to n.c. Minn.; s.e. to so. Ill. and cen. Ohio (Figs. 1a, 9a).

While it has not been possible to see the original Linnaean type, or reproductions of it, examination of an illustration[12] of excellent quality in Dillenius, Hortus Elthamensis, cited by Linnaeus (6), provides clear and unmistakable evidence that the ssp. *eupensylvanica* as herein understood, is equivalent to the original Linnaean species. The oblanceolate, entire to denticulate leaves, the linear-lanceolate petals, the rather slender follicles, and particularly the cymose-paniculate inflorescence of rather congested, conglomerate cymules are quite like material of ssp. *eupensylvanica* from open meadow habitats throughout the range. Specimens seen from Pennsylvania, given by Small and Rydberg (10) as the type locality, and from the rest of the range, are quite similar in the respects cited above to that illustrated in Dillenius. Comparison of Figs. 3a and 10 will conclusively confirm this statement. In none of the other expressions of this polymorphic species does this combination of characters occur.

Representative specimens:[13]—NEW HAMPSHIRE: Rockingham Co., Derry, W. H. Seaman (USNM 787969); MASSACHUSETTS: Essex Co., Ipswich, W. Oakes (UW); Middlesex Co., So. Framingham, 1890, Sturtevant, (MBG 84497); Suffolk Co., Boston,

12 T253, f328, herein reproduced as Fig. 10.

13 Herbaria from which specimens were obtained for study are designated herein as follows: UM, University of Minnesota; USNM, United States National Museum; MBG, Missouri Botanical Garden; UI, University of Illinois; UW, University of Wisconsin; UP, University of Pennsylvania.

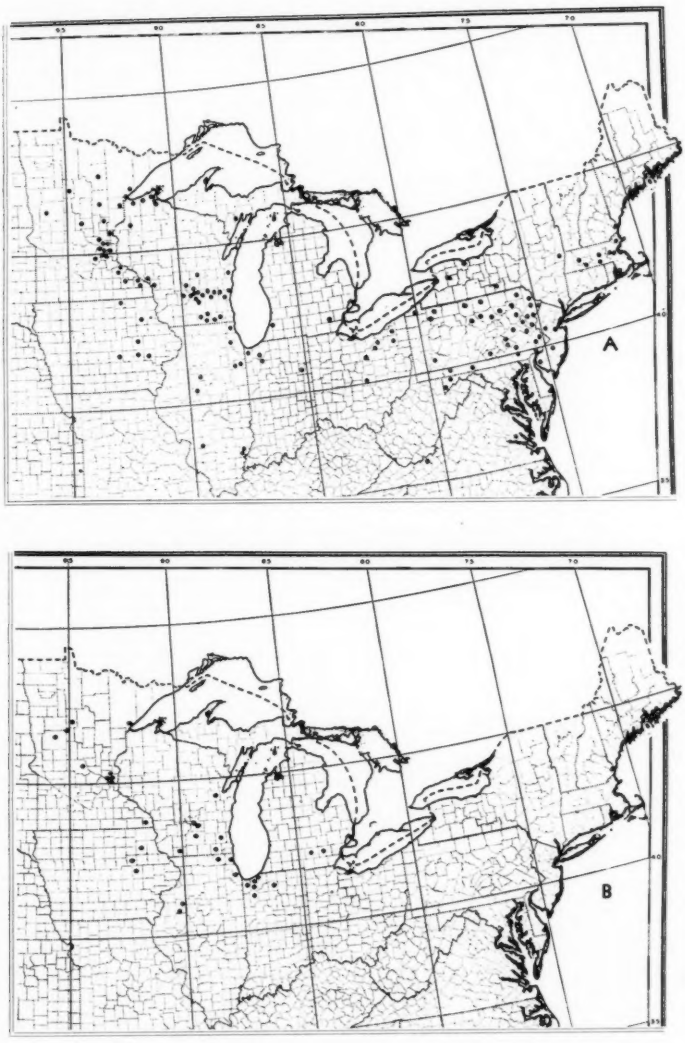

Fig. 9. Distribution maps for specimens examined: A. *S. pensylvanica*, ssp. *eupensylvanica*; B. *S. pensylvanica*, ssp. *interior*, var. *crassicarpa*.

1816, F. Boot, (USNM 1394007); Norfolk Co., Canton, May 31, 1909, S. F. Blake, (USNM 1088558); Worcester Co., Uxbridge, May 28, 1875, (USNM 139466); Hampshire Co., Hadley, May, 1870, G. C. Woolson, (UI); Hampden Co., W. Holyoke, May 14, 1925, F. C. Seymour 478, (MBG 927686); RHODE ISLAND: Providence Co., Providence, Cat Swamp, May 24, 1900, E. B. Chamberlain 88, (USNM 491080); CONNECTICUT: Tolland Co., Storrs, May 30, 1924, C. A. Weatherby, (USNM 1288298); Middlesex Co., Middletown, (USNM 772170); NEW YORK: Columbia Co., 1 mi. n. Kinderhook, R. C. McVaugh 977 (UP); Madison Co., Pecksport, June 9, 1916, W. R. Maxon 6216, (USNM 789505); Tompkins Co., Ithaca, July 11, 1920, W. C. Muenscher, A. R. Bechtel, (USNM 1240345); Genesee Co., Pavilion, May 31, 1862, ex herb. E. J. Hill, (UI); NEW JERSEY: Sussex Co., btw. Hamburg and Stockholm, May 19, 1894, C. L. Pollard, W. Van Sickle, (USNM 310662); Hunterdon Co., Grover, May 25, 1894, ex herb. H. L. Fisher 999, (UW); Monmouth Co., Farmingdale, Long and Brown 3684, May 28-30, 1910, (UP 62099); Burlington Co., 2 mi. n.e. Camp Dix, May 8, 1938, L. P. Hynes, (UP); Camden Co., Lindenwold, June 5, 1904, W. Stone, (UP); Gloucester Co., Sewell, J. M. Macfarlane, May 11, 1906, (UP 42002, 42003); Salem Co., 1 mi. s.w. Woodstown, May 6, 1935, J. M. Fogg, Jr. 8176 (UP).

PENNSYLVANIA: Wayne Co., Evans Falls, Glowenke 1496, (UP); Pike Co., Bushkill Falls, June 26, 1915, J. W. Eckfeldt, (UP); Monroe Co., Merwinsburg, cold stream foot of mountains, June 10, 1923, J. M. Fogg, Jr. 420, (UP 75186); Northampton Co., 1¼ mi. e. Hellertown, Apr. 29, 1936, F. J. Trembley, (UP); Bucks Co., Nockamixon Rocks, Oct. 23, 1908, J. W. Harshberger (UP 49092); Montgomery Co., 1½ mi. s.w. Green Lane, May 11-12, 1935, Travis, (UP); Philadelphia Co., Germantown, Gorgas Lane, May 19, 1899, (USNM 958446); Delaware Co., Swarthmore, May 27, 1888, (UP 7480); Chester Co., W. W. Jefferies, (USNM 204197); Susquehanna Co., Lynn, Glowenke 2238, (UP); Wyoming Co., w. shore Susquehanna Riv., May 29, 1937, Glowenke 217, (UP); Sullivan Co., 2 mi. n.w. Murray Valley, June 7, 1938, Wagner 6716, (UP); Luzerne Co., 2.5 mi. n.w. Conyngham, June 10, 1938, J. M. Fogg Jr. 14574, (UP); Schuylkill Co., vic. Drehersville, May 27, 1939, Wagner 7894, (UP); Lebanon Co., Mt. Gretna, May 30, 1914, C. H. Arndt, (UP); Lancaster Co., s.e. Beartown, June 6, 1940, Tanger, (UP); Tioga Co., 5 mi. e.n.e. Mainesburg, June 15, 1936, F. S. Fender 1541, (UP); Lycoming Co., Montoursville, May 22, 1930, (UP); Cumberland Co., Hunters Run, May 11, 1921, Gress, (UP); York Co., May 25, 1895, N. M. Glatfelton, (MBG 84491); Fulton Co., June 4, 1905, Stone, (UP); Warren Co., s. Sulphur Spring, June, 1934, Mathias, (UP); Westmoreland Co., May 30, 1877, Pierron, (USNM 139465); Somerset Co., Salisbury, June 27, 1934, True 126, (UP); Allegheny Co., Harrison Twp., June 2, 1892, Koenig, (USNM 364849); MARYLAND: Garrett Co., Jennings, June 25, 1907, Stone, (UP); VIRGINIA: James City Co., n.e. Williamsburg, Mar. 28, 1921, Grimes 3353, (UM 178353); Giles Co., 2¼ mi. s.w. Kire, Aug. 5, 1937, Fogg Jr. 12960, (UP).

OHIO: Geauga Co., Geauga Lake, June 2, 1894, L. D. Straw, (USNM 307940); Stark Co., Canton, May 23, 1896, Straw, (MBG 84489); Medina Co., Liverpool, June, 1896, Watson, (UM 178388); Lorain Co., May 21, 1891, Kofoid, (USNM 892351); Richland Co., Mansfield, May 20, 1885, Wilkinson, (USNM 958402); Franklin Co., Columbus, (UW); MICHIGAN: Washtenaw Co., Ann Arbor, May 28, 1860, ex herb. Dean, (MBG 84492); Shiawassee Co., Owosso, May 17, 1889, Hicks, (USNM 61284); Delta Co., Escanaba, June 21, 1927, E. Anderson, R. E. Woodson Jr. 1688, (MBG 979536); Marquette Co., Turin, June 13, 1901, Barlow, (USNM 416097); INDIANA: Wells Co., Lancaster Twp., Sec. 32, May 26, 1905, C. C. Deam, (USNM 493267); Marshall Co., nr. L. Maxinkuckee, May 22, 1901, Clark 1700, (USNM 407533); Lake Co., Miller, May 26, 1918, Kienholz, (UI); ILLINOIS: Wabash Co., Mt. Carmel, May 24, 1877, ex herb. Schneck 313, (UI); St. Clair Co., Mascoutah, ex herb. Welsch, (UI); Peoria Co., Peoria, (UI); Kankakee Co., June 5, 1908, (UI 28600); Du Page Co., Wheaton, May 19, 1889, ex herb. Moffatt 266,

(UI); Lake Co., Lake Forest, Nash, (UW); Wadford Co., June 1887, McDonald, (UI); WISCONSIN: Walworth Co., nr. Bloomfield, June 3, 1925, Palmer 27557, (MBG 950970); Rock Co., 8 mi. w. Beloit, May 13, 1928, Fassett 5790, (UW); Milwaukee Co., Milwaukee, Lapham, (UW); Jefferson Co., May 30, 1929, Allen 218, (UW); Dane Co., Madison, Univ. Bay, June 21, 1907, ex herb. Heddle 406, (UW); Washington Co., Hartford, July 9, 1929, Quandt 229, (UW); Dodge Co., Reeseville, June 13, 1931, Rhodes 158, (UW); Sauk Co., Devils Lake, June 4, 1926, Kraus and Baxter, (UW); Richland Co., 1½ mi. n.e. Ithaca, May 18, 1930, Fernholz, (UW); La Crosse Co., Mormon Coulee, June 10, 1930, Hansen 400, (UW); Manitowoc Co., Pigeon Lake, May 30, 1930, Smith 281, (UW); Brown Co., Green Bay, May 18, 1878, J. H. Schuette, (USNM 751770); Ashland Co., Ashland, May 23, 1930, Bobb 91, (UW); Washburn Co., Chittamo, June 20, 1929, Fassett 8664, (UW); IOWA: Johnson Co., Iowa City, (MBG 84498); Powshiek Co., nr. Grinnell, May 21, 1886, (MBG 84482); Black Hawk Co., June 4, 1929, Burk 290, (MBG 985576); Fayette Co., May 15, 1894, ex herb. B. Fink, (USNM 203390); MINNESOTA: Winona Co., Winona, June 1, 1888, Holzinger, (UM 178378); Olmsted Co., Rochester, May 24, 1902, Ainslee, (UM 178373); Wabasha Co., nr. Lake City, July 1, 1878, ex herb. Manning, (UM 178366); Washington Co., s. of St. Croix village, June 5, 1920, Butters, Rosendahl, Johnson, (UM 178370); Ramsey Co., 1 mi. n.e. Lake Johanna, June 18, 1919, Rosendahl 3808, (UM 178352); Hennepin Co., Lake Harriet, Minneapolis, June 20, 1895, Moyer and Manning, (UM 178351); Mille Lacs Co., Milaca, July, 1892, Sheldon, (UM 178379); Morrison Co., June 15, 1910, Chandonnet, (UP 60440); Ottertail Co., Perham, June 21, 1912, Chandonnet, (MBG 830478); Hubbard Co., btw. Bemidji and Itasca Park, July 3, 1933, Moyle, (USNM 1630538); Aitkin Co., Nichols, June, 1892, Sheldon, (UM 178356); Itasca Co., Bowstring, June and July, 1925, Stark 1189, (UM 229026); St. Louis Co., Knife River, June, 1893, Sheldon, (UM 178376).

2. **S. pensylvanica** L., ssp. **eupensylvanica** ssp. nov., f. **fultior** (Fernald) comb. nov.

Syn.: S. pennsylvanica L., f. *fultior* Fernald, Rhodora **19**: 144. 1917.
S. pennsylvanica L., var. *fultior* (Fernald) Bush, Amer. Midl. Nat. **11**: 230. 1928.

"Lower bracts dilated, oval, 7-10 cm. long, 4.5-7 cm. wide," (Fernald, *loc. cit.*). Otherwise like *S. pensylvanica,* ssp. *eupensylvanica.*

Habitat: as for ssp. *eupensylvanica.*

Distribution in U. S.: occasional throughout the range of ssp. *eupensylvanica.*

Apparently a single gene mutant, distinctive solely through the foliaceous bracts of the inflorescence, and having no geographic range of its own.

Specimens examined:—MASSACHUSETTS: Middlesex Co., Waltham, May 16, 1897, J. M. Greenman 632, (MBG 738765); NEW YORK: Tompkins Co., Ithaca, May 18, 1879, ex herb. W. A. Henry, (UW); Rush, May 25, 1926, W. A. Matthews 2564, (UW); PENNSYLVANIA: Lebanon Co., May 27, 1893, A. A. Heller and E. G. Halbach 872, (UM 178350); OHIO: Stark Co., Canton, June, 1835, J. Riehl, (MBG 84245); WISCONSIN: Waushura Co., Lunch Cr., May 21, 1938, N. C. Fassett 19887, (UW).

3. **S. pensylvanica** L., ssp. **eupensylvanica** ssp. nov., var. **purpuripetala** (Johnson) comb. nov.

Syn.: S. purpuripetala Johnson, Minn. Studies Pl. Sci. **4**: 51, 1923.
S. pennsylvanica L., var. *purpuripetala* (Johnson) Bush, Amer. Midl. Nat. **11**: 229. 1928.

Fig. 10. *S. pensylvanica*, as illustrated in Dillenius, *Hortus Elthamensis* (1732) and cited by Linnaeus (6). Compare with ssp. *eupensylvanica*, Fig. 3, A.

Leaves in a basal rosette, persisting over winter, to 2 dm. long, 2.5-5.0 cm. wide, entire to denticulate, acute or occasionally rounded at the apex, tapering below into a margined petiole 1-5 cm. long; blades dark green above, lighter below, leathery, glabrous.

Inflorescence cymose-paniculate, scape to 6 dm. high, glandular-pilose, the glands purple; sparingly branched, the branches to 7 cm. long, in the axils of linear, entire to denticulate bracts to 2 cm. long, flowers 6-9 mm. in diameter, in open, rather few-flowered cymules.

Sepals green to occasionally purplish-green, deltoid to narrowly triangular, acute, distant, slightly united at the bases, 2-2.3 mm. long, 1.0-1.7 mm. wide, costate, with 2 obsolescent laterals, the midrib continuing to the apex or appearing to stop short of the apex, tips purplish or dark, reflexed at anthesis, becoming somewhat appressed in fruit; petals dark reddish purple, linear to lance-linear, 2-3 mm. long, .3-.5 mm. wide, acute, 1-nerved; filaments purple, subulate, 1.2-1.7 mm. long, slightly incurved at the apex at anthesis. Hypanthium adnate to the bicarpellate ovary 1/5 - 1/4 above the base; ovary enclosed at anthesis nearly to the summit by a broad, verrucose, rugose, greenish or purplish nectary which persists as an obsolete ring around the base of the carpels about .5 mm. above the point of their adnation to the hypanthium. Carpels united at the bases only, separate above, follicular in fruit, dilated below and tapering rather abruptly to the short (.5 mm.) stout, divergent (45°-90°) obscurely veined and purplish styles; stigmas dark, capitate. Seeds brown, with a slight constriction at each end, tuberculate, carinate along one side, 1.2 mm. long, .45 mm. wide (Fig. 11).

Chromosome number: n=28. (Fig. 2.).

Habitat: bogs, swamps and wet ditches, chiefly in shade.

Distribution in U. S.: no. N. H. and Vt., so. to cen. N. J. and s.w. Me., w. to extreme e. N. Y. and Penn. (Fig. 1a, b.)

Differs from *S. pensylvanica,* ssp. *eupensylvanica* chiefly in the stouter, shorter styled fruits, narrower petals, longer and narrower sepals, the slightly larger seeds, the purple coloration which extends throughout all the floral parts, and the dark, leathery, glabrous leaves. Probably a multiple gene mutant. Hybridizes with ssp. *eupensylvanica* in eastern New York, Pennsylvania and in Delaware.

Specimens examined:—MAINE: York Co., So. Berwick, Aug. 19, 1936, R. H. True 2494, (UP); York Co., No. Berwick, June 24, 1938, O. M. Neal Jr. 1355, (UP); May 30, 1874, ex herb. F. L. Scribner, ex herb. J. B. Brinton, (UP7479); York Co., Sep. 6, 1936, R. H. True 2689a, (UP); NEW HAMPSHIRE: Grafton Co., Hanover, June 9, 1883, C. H. Hitchcock, ex herb. Darmouth Coll., (UM 178333); Grafton Co., Hanover, May, 1927, J. H. Fassett, (UW); VERMONT: Caledonia Co., Ryegate, June 15, 1883, F. Blanchard, (MBG 751773); Addison Co., Monkton, May 14, 1878, C. G. Pringle, (USNM 61285); New Haven Swamp, June 8, 1883, (USNM 139463); "western Vt.," May 24, 1896, W. W. Eggleston, specimens a and b, (UM 259256); Caledonia Co., Peacham, May, 1895, E. E. Gayle 705, (USNM 237777); Caledonia Co., Peacham, June 3, 1883, F. Blanchard, (MBG 751772); Caledonia Co., Peacham, Aug., 1892, F. Blanchard, (MBG 751775); Caledonia Co., June 13, 1884,

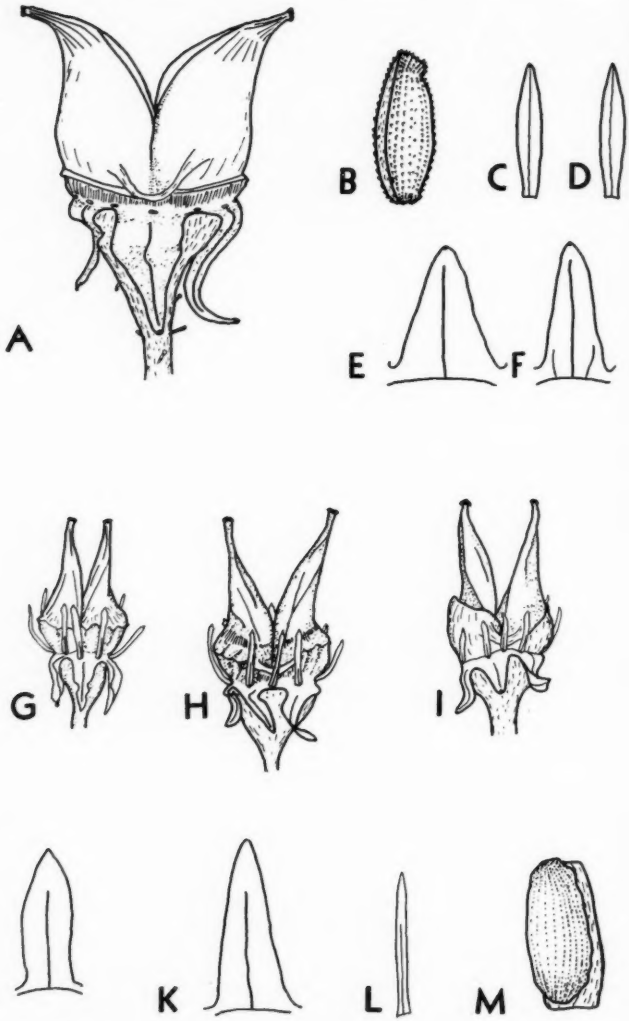

Fig. 11. A-F. *S. pensylvanica*, ssp. *eupensylvanica*, var. *purpuripetala*. A. mature *follicles* (×10); B. seed (×20); C, *D. petals* (×10); E, F. sepals (×10); G-M. ssp. *tenuirostrata:* G-I. mature follicles (×5); J, K. sepals (×7); L. filament (×10); M. seed (×20).

F. Blanchard, (MBG 751771); Middletown, June 7, 1930, D. S. Carpenter, (UM 279097); Rutland Co., Rutland, May 24, 1896, W. W. Eggleston, (USNM 363144); MASSACHUSETTS: Middlesex Co., Somerville, May 26, 1879, ex herb. W. H. Manning 852, (UM 178384); Berkshire Co., Washington, June 7, 1878, J. W. Redfield, (MBG 84473); Berkshire Co., Washington, June 7, 1878, Redfield, 2nd sheet, (MBG 84474); CONNECTICUT: Tolland Co., Storrs, May, 1907, ex herb. W. W. Ohlmeiler, (MBG 792269); Hartford Co., Southington, May 14 and June 2, 1897, C. H. Bissell, (MBG 84487); Tolland Co., Storrs, May 19, 1940, M. T. Travis 2127, (UP); NEW YORK: Delaware Co., No. Harpersfield, D. L. Topping 172, (USNM 647384); Tompkins Co., Ithaca, Ellis Hollow, June, 1891, W. W. Rowlee, (USNM 226249); Malloryville, June 2, 1877, W. Trelease, (MBG 84499); NEW JERSEY: Bergen Co., Fairview, May 13, 1895, (USNM 246415); Passaic Co., May 30, 1895, ex herb. E. W. Berry, (UI); Somerset Co., near Peapack, ex herb. R. C. Perry, (MBG 84563); Sussex Co., Montague, May 17, 1936, R. H. True 1839, (UP); PENNSYLVANIA: Pike Co., May 7, 1938, P. dePue 33, (UP).

4. S. pensylvanica L., ssp. eupensylvanica ssp. nov., var. purpuripetala (Johnson) comb nov., f. bractealis f. nov.

Bracteis inferioribus foliaciis, lanceolatis vel ovatis, 2-5 cm. longis, .75-1.5 cm. latis.

Lower bracts foliaceous, lanceolate to ovate, 2-5 cm. long, .75-1.5 cm. wide. Otherwise like *S. pensylvanica*, ssp. *eupensylvanica*, var. *purpuripetala*.

Habitat: as for var. *purpuripetala*.

Distribution in U.S.: occasional with var. *purpuripetala*.

Apparently a single gene mutant, differing from var. *purpuripetala* only in the foliaceous inflorescence bracts, and without a distinctive range.

Specimens examined:—VERMONT: Rutland Co., Rutland, May 16, 1896, ex herb. W. W. Eggleston, (UM 178347); Rutland Co., Rutland, W. W. Eggleston, (UM 259257); MASSACHUSETTS: Middlesex Co., Waltham, ex herb. J. M. Greenman 2896, *type*, (MBG 737860); Bradford, ex herb. M. L. Goss, (UI); NEW YORK: Tompkins Co., s.w. Groton, May 15, 1889, ex herb. E. L. Sturtevant, ex herb. W. W. Rowlee, (MBG 84496).

5. S. pensylvanica L., ssp. tenuirostrata ssp. nov.

Folia basalia 15-25 cm. longa, 3-5 cm. lata, lanceolata, integra vel denticulata, tomentosa; caulis floriferus scapiformis, ad 10 dm. altus; rami primarii inflorescentiae adscendentes, ad 1 dm. longi; sepala anguste triangularia vel deltoidea, 3-4 mm. longa, 1 mm. lata, reflexa, petala plerumque virella, rare alba, linearia, 3-3.5 mm. longa, .5 mm. lata, uninerva, filamenta linearisubulata, 2-2.5 mm. longa; ovaria 1/3 - 1/2 inferiora, carpella follicularia chartacea, erecta vel ad 90° divergentia, infra valde inflata, supra gracilia attenuataque, semina fusca tuberculata, unilateraliter carinata, ovoidea.

Leaves in a basal rosette, persisting over winter, to 25 cm. long, 3-5 cm. wide, lanceolate, entire to denticulate, densely tomentose on both surfaces, the hairs subulate, lax, to 2 mm. long; tapering below to a narrow, margined petiole to 5 cm. long.

Inflorescence cymose-paniculate, the ascending branches to 1 dm., in the

axils of linear, entire to denticulate bracts; flowers in congested cymules. Scape to 10 dm. high, glandular-pilose.

Sepals green, narrowly triangular or occasionally deltoid, 3-4 mm. long, 1 mm. wide, 1-3-nerved, reflexed; petals white or occasionally greenish-white, linear, 3-3.5 mm. long, .5 mm. wide, 1-nerved; filaments linear-subulate, 2-2.5 mm. long, incurved at the apex at anthesis; at least some of the anthers lemon-yellow. The bicarpellate ovary rather deeply inferior in fruit, 1/3 - 1/2 the length of the carpels, the nectary persisting in fruit as a prominent ridge surrounding the carpels about 1 mm. above the point of their adnation to the hypanthium; carpels follicular in fruit, thin, erect or divergent to 90°, strongly inflated just above the point of their adnation to the hypanthium, slender and long-tapering above. Styles .5-1.5 mm. long; stigmas small, capitate or flattened. Fertility erratic; seeds, when present brown, tuberculate, carinate along one side, oval, not markedly constricted at each end (Figs. 4a, 11).

Chromosome number: n=42. (Fig. 2).

Habitat: bogs and wet meadows.

Distribution in U. S.: not definitely known as yet; known only from Minn. where it is occasional, but locally abundant, with both sspp. *eupensylvanica* and *interior*.

Unique through the longer, more slender carpels which remain deeply inferior in fruit, tomentose leaves and erratic fertility, as well as hexaploid chromosome number. Probably an intra-specific chromosome race hybrid of the cross ssp. *eupensylvanica* x ssp. *interior*. To be expected, then, within the joint ranges of those subspecies.

Specimens examined:—MINNESOTA: Ramsey Co., 1½ mi. n.w. Turtle Lake, June 16, 1941, G. W. Burns 400, *type* (UM 36843[1]); Carver Co., Chaska, June, 1891, C. A. Ballard, (UM 178377); Clearwater Co., n.e. of U. M. Forestry School, Itasca Park, July 13, 1929, M. L. Grant 2764 (UM276075).

6. S. pensylvanica L., ssp. interior ssp. nov., var. crassicarpa (Johnson) comb. nov.

Johnson, Minn. Studies Pl. Sci. **4**: 43. 1923.

Syn.: ?*S. semipubescens* Sweet, Hort. suburb. 97. 1818.
?*S. semipubescens* D. Don, Trans. Linn. Soc. **13**: 385. 1822.
S. crassicarpa Johnson, Minn. Studies Pl. Sci. **4**: 43. 1923.
S. pennsylvanica L., var. *crassicarpa* (Johnson) Bush, Amer. Midl. Nat. **11**: 228. 1928.
S. pennsylvanica L., var. *dichotoma* Bush (in part), Amer. Midl. Nat. **11**: 231. 1928.

Leaves in a basal rosette, persisting over winter, ovate or occasionally somewhat lanceolate, 9-31 cm. long, 3-10 cm. wide, length-width ratio ca. 3.4:1, entire to denticulate, tapering below to a short, margined petiole, 1-3 cm. long; blades variously hirsute above or below, or both, the hairs subulate, lax, 2-3 mm. long.

Inflorescence cymose-paniculate, scape stout, to 10 dm. high, glandular-pilose, often densely so, the branches ascending or divergent, to 12 cm. long, in the axils of linear, entire to denticulate bracts to 2 cm. long, 2-5 mm. wide; flowers 7-10 mm. in diameter, in rather few-flowered cymules, becoming somewhat distant in fruit.

Sepals green, deltoid to ovate-triangular, acute or occasionally rounded at the apex, slightly united at the bases, 1.5-2.0 mm. long, 1.5-2.0 mm. wide, 1-nerved or occasionally with 2 short, obsolescent laterals, reflexed-appressed; petals white or greenish-white, ovate or occasionally lanceolate, 3-nerved, 2-3 mm. long, 1-1.5 mm. wide; filaments subulate, 1-1.5 mm. long, incurved at the

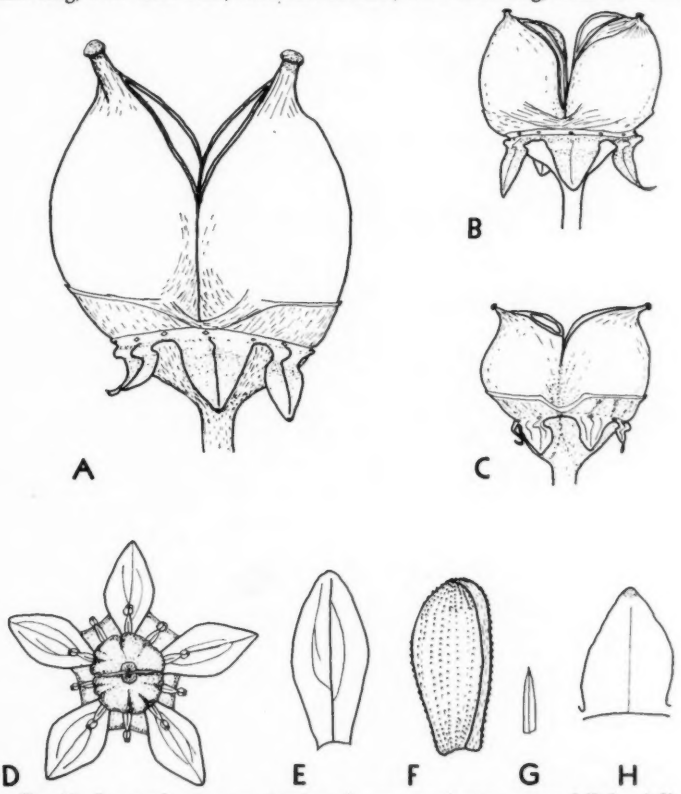

Fig. 12. *S. pensylvanica*, ssp. *interior*: A. var. *crassicarpa*, mature follicles (×8); B. var. *winnebagoensis*, mature follicles (×8); C. var. *congesta*, mature follicles (×4); E. petal (×8); F. seed (×20); G. filament (×8); H. sepal (×8). A, B, C, and F drawn from respective type specimens.

apex at anthesis, anthers reddish-orange. Hypanthium adnate to the bicarpellate (frequently tri- or tetracarpellate) ovary 1/7 to 1/5 above the base; ovary enclosed by a broad, verrucose, somewhat rugose, greenish-yellow nectary at anthesis, the nectary persisting in fruit as an obsolete ridge around the base of the carpels .5-.7 mm. above the point of their adnation to the hypanthium. Carpels united for the lowermost 1/7 - 1/5, separate above, slightly or not at all divergent, follicular in fruit, about 4-5.5 mm. long and 4-5 mm. wide above the point of their adnation to the hypanthium, stout throughout their length, surmounted by a short (ca. .5 mm.) divergent (22°-67°) style; stigmas capitate, globose. Seeds brown, tuberculate, carinate along 1 side, large (1.3 mm. long, .65 mm. wide). (Figs. 4b, 12).

Chromosome number: n=56. (Fig. 2).

Habitat: bogs and wet meadows.

Distribution in U. S.: s.e. Mich. to n.c. Minn., so. to cen. Ill. and Ind. (Fig. 1a, 9b.)

Characterized by shorter, broader leaves and floral parts, the large, inflated fruits, and larger seeds, as well as few-flowered, coarse inflorescence, and octoploid chromosome number.

Specimens examined:—MICHIGAN: Washtenaw Co., Ann Arbor, May 17, 1921, J. H. Ehlers 1471, (UI); Jackson Co., May 30, 1896, ex herb. Camp, (UM 178364); Cedar Sprs., May 22, 1897, C. W. Fallass, (USNM 958400); INDIANA: Jasper Co., Wheatfield, June 17, 1924, W. Welch, plant a only, (UI); Porter Co., McCool, June 13, 1910, E. J. Hill, plant b only, (UI); Lake Co., Miller, May 30, 1902, A. Chase, (UI); Lake Co., Miller's, May 14, 1898, L. M. Umbach 8449, (UW); Mt. Tom, May 8, 1915, Kienholz, (UI); ILLINOIS: Stark Co., nr. Wady Petra, May 12, 1897, V. H. Chase, (MBG 84469); Stark Co., May 12, 1897, V. H. Chase, (UI); Kankakee Co., vic. Kankakee, May 12, 1913, C. C. Crampton 79, (USNM 750654); Cook Co., nr. Chicago, June 26, 1892, ex herb. W. S. Moffatt, (UM 178383); Beach, June 5, 1909, L. M. Umbach 3183, (UW 33200); IOWA: Benton Co., Vinton, J. G. Davis, (UW); Fayette Co., Fayette, May 1894, B. Fink, (UW); Black Hawk Co., June 4, 1929, M. Burk 290, (UI); WISCONSIN: Walworth Co., East Troy, 2 coll. July 4 and Aug. 4, 1926, L. Almon, (UW); Walworth Co., Whitewater, May 26, 1882, N. Sykes, (UW); Green Co., Monroe, May 30, 1890, S. C. Stuntz, (UW); Milwaukee Co., Milwaukee, ex herb. C. Mohr, (USNM 772169); Waukesha Co., Big Bend, May 30, 1931, N. C. Fassett 13861, (UW); Dane Co., Madison, T. J. Hale, (UW); Outagamie Co., Appleton, June 13, 1928, A. H. Smith 217, (UW); Barron Co., Barron, June 16, 1889, L. S. Cheney, (UW); McHenry Co., April and May, 1932, L. Heider, (UW); MINNESOTA: Ramsey Co., 1 mi. n.e. L. Johanna, June 18, 1919, C. O. Rosendahl 3810, (UM 178368); Ramsey Co., 1 mi. n.e. L. Johanna, June 18, 1919, C. O. Rosendahl 3809, (UM178367); Hennepin Co., Minneapolis, May, 1894, J. H. S. 4642, (UW); Hennepin Co., May 12, 1891, F. H. Burglehaus, (UM 178362); Hennepin Co., May, 1890, J. H. Sandberg, (UM 178354); Pope Co., Groveland, May 10, 1914, F. J. Piemeisel, (UM 288274); Ottertail Co., June 19, 1921, Johnson, Butters and Rosendahl, plants 1 and 2 only, (UM 178348); Hubbard Co., July 3, 1933, J. B. Moyle 748, (MBG 1077865); Beltrami Co., June 19, 1912, J. A. S. 29, (UM265647); Beltrami Co., Bemidji, June 19, 1912, J. A. S. (UM 265640); St. Louis river (St. Louis Co.?) July 23, 1886, Arthur, Bailey, Holway, *type*, (UM 178423).

7. **S. pensylvanica** L., ssp. **interior** ssp. nov., var. **crassicarpa** (Johnson) comb. nov., f. **bracteata** f. nov.

Bracteis inferioribus foliaciis, ovatis, 2.5-6.0 cm. longis, 1.0-2.5 cm. latis.

Lower bracts foliaceous, ovate, 2.5-6.0 cm. long, 1.0-2.5 cm. wide. Otherwise similar to var. *crassicarpa*.

Habitat: as for var. *crassicarpa*.

Distribution in U. S.: occasional throughout the range of var. *crassicarpa*.

Apparently a single gene mutant, differing only as to inflorescence bracts, and without distinctive range.

Specimens examined:—INDIANA: Porter Co., Dune Park, May 15, 1909, ex herb. L. M. Umbach 2889, (UW 33201); ILLINOIS: Stark Co., e. of Wady Petra, May 12, 1897, V. H. Chase, (UI); MINNESOTA: Apr. 1890, E. L. Morris, *type*, (UM 178349).

8. **S. pensylvanica** L., ssp. **interior** ssp. nov., var. **congesta** var. nov.

Folia basalia 15 cm. longa, 5 cm. lata, obovata, interdum tantum spatulata, crenulata vel dendiculata, hirsuta; caulis floriferus ad 6 dm. altus, ramis primariis ad 6 cm. longis, adscendentibus; cymulae congestae, multifloriferae, sepala deltoidea, 1mm. longa, 1mm. lata, trinervata, petala plerumque alba rare subviridia, lanceolata vel ovato-lanceolata, trinervata, 2 mm. longa, 1 mm. lata, filamenta subulata, 1-2 mm. longa; ovaria in fructu tantum superioria, carpella follicularia parce divergentia, crassa, 1 mm. longa, 2 mm. lata, semina fusca, tuberculata, unilateraliter carinata, .9 mm. longa, .36 mm. lata.

Leaves in a basal rosette, persisting over winter, 15 cm. long, 5 cm. wide, obovate or occasionally nearly spatulate, margin crenulate to denticulate, obtuse or rounded at the apex, tapering below to a short (1-4 cm.) margined petiole; blades hirsute above and below, especially toward the base, the hairs linear to subulate, to 2 mm. long.

Inflorescence cymose-paniculate, to 6 dm. high, sparingly branched, the branches to 6 cm. in the axils of the obsolescent linear bracts to 5 mm. long; flowers numerous, in densely congested cymules.

Sepals green, deltoid, acute, slightly united at the bases, 1 mm. long, 1 mm. wide, costate, with 2 less prominent laterals, reflexed-appressed; petals white or greenish-white, lanceolate to lance-ovate, 3-nerved, 2 mm. long, 1 mm. wide; filaments subulate, 1-2 mm. long, incurved at the apex at anthesis. Hypanthium adnate to the bi-carpellate, or occasionally tri-carpellate, ovary at the very base. Ovary at anthesis enclosed by a broad, rugose, greenish-yellow nectary which persists in fruit as an obsolete ridge around the bases of the carpels about .5 mm. above the point of their adnation to the hypanthium. Carpels united at the extreme base only, separate above, slightly or not at all divergent in fruit, follicular, 1 mm. long, 2 mm. wide above the hypanthium, stout, inflated throughout, styles .5 mm. long, divergent 22°-45°; stigmas capitate, flattened. Seeds brown, tuberculate, carinate along one side, in appearance resembling those of var. *crassicarpa* but smaller, .9 mm. long, .36 mm wide. (Figs. 4c, 12b).

Chromosome number: n=56.

Habitat: bogs and wet meadows.

Distribution in U. S.: known from Wis. to Minn.

Distinctive through the smaller fruits and seeds, the more floriferous, congested inflorescence and in leaf shape.

Specimens examined:—WISCONSIN: Walworth Co., nr. Lake Beulah, July 26, 1905, J. I. Shannon, (MBG 84478); MINNESOTA: Ramsey Co., 1 mi. n.e. Lake Johanna, June 18, 1919, C. O. Rosendahl 3811, (UM 178369); Ramsey Co., 1½ mi. n.w. Turtle Lake, June 16, 1941, G. W. Burns 456, *type*, (UM 368432).

9. S. pensylvanica L., ssp. interior ssp. nov., var. winnebagoensis (Johnson) comb. nov.

Syn.: S. winnebagoensis Johnson, Minn. Studies Pl. Sci. **4**: 53. 1923.
S. pennsylvanica L., var. *winnebagoensis* (Johnson) Bush, Amer. Midl. Nat. **11**: 230. 1928.

Leaves in a basal rosette, narrowly oblong, 5-13 cm. long, 1-3 cm. wide, without prominent lateral veins, yellowish-green, sparsely hirsute, chiefly on the upper surface, the hairs lax, subulate, about 1 mm. long; margin entire to obscurely denticulate, tapering below to a short margined petiole, 1-2 cm. long.

Inflorescence spicate or occasionally somewhat cymose-paniculate, to 5.5 dm., pilose, strict, bearing a few divergent branches 1-3 cm. long, in the axils of linear bractlets to 2 cm. long. Cymules few-flowered, somewhat congested.

Sepals green, deltoid, acute or sometimes slightly rounded at the apex, 1.5 mm. long, 1.5 mm. wide, 1-3 nerved, reflexed-appressed; petals lanceolate to lance-ovate, white, 3-nerved, 1.5 mm. long, .5 mm. wide, filaments subulate, acuminate, 2 mm. long. Hypanthium rather shallow, adnate to the bi-carpellate ovary about 1/5 above its base; carpels united at the extreme bases only, follicular in fruit. Follicles small, 2.5 mm. long, 1.5 mm. wide, globose, inflated, the stigmas small, capitate, and nearly sessile; styles .5 mm. or less; fruits and styles scarcely divergent. Nectary disappearing in fruiting stages. Seeds brown, fusiform, ridged, somewhat tuberculate, inconspicuously carinate along one side, 1 mm. long, .4 mm. wide. (Figs. 4d, 12b).

Chromosome number: probably n=56.

Habitat: bogs and wet meadows.

Distribution in U. S.: probably occasional, Ind. n.w. to Minn.

Characterized by few-flowered, short, spicate cyme, the small sub-globose follicles with sessile stigmas, and yellowish-leaves.

Specimens examined:—INDIANA: Clarke, May 25, 1895, L. M. Umbach 221, ex herb. Northwestern College, (UM 178382); MINNESOTA: Houston Co., Winnebago valley, June 9, 1893, ex herb. W. A. Wheeler 73, (UM 270053); Houston Co., Winnebago valley, June 12, 1899, W. A. Wheeler 180, *type*, (UM 178327).

10. S. FORBESII Vasey, Amer. Entomol. & Bot. **2**: 288. 1870.

Rosendahl, Engl. Bot. Jahrb. **37**, Beibl. 83: 67. 1905.
Robinson & Fernald, Gray's New Man. Bot., ed. 7, 446. 1908.

Syn.: Micranthes Forbesii (Vasey) Bush, Mo. Bot. Gard. Rept. **20**: 138. 1909.

S. pennsylvanica L., var. *Forbesii* (Vasey) Engl. & Irm., Pflanzenreich *IV*(117): 66. 1916.

S. pennsylvanica L., var. *Forbesii* (Vasey) Bush, Amer. Midl. Nat. **11**: 231-2. 1928.

Leaves in a basal rosette, persisting over winter, sparsely and coarsely hirsute on both sides, the lax, subulate hairs on the upper surface each arising from a small papilla, entire to distantly denticulate, lanceolate to lance-ovate, 10-20 cm. long, 3-7 cm. wide, acute, tapering below to a short, margined petiole, .5-4.0 cm. long.

Inflorescence a lax and open paniculate cyme, scape to 6 dm., glandular-pilose, branches few, to 15 cm. long, divergent or ascending, often equalling the summit of the scape, in the axils of linear, entire to denticulate bracts to 15 mm. Flowers 6-10 mm. in diameter, in open, rather few-flowered cymules.

Sepals green, deltoid, 1.5-2.0 mm. long, 1.5-2.0 mm. wide, acute, or rounded at the apex, 3-nerved, reflexed at anthesis, appressed-recurved in fruit; petals ovate to lance-ovate, white, 3-nerved; filaments subulate, 1.5 mm. long. Hypanthium adnate to the bi-carpellate ovary 1/5 above its base; ovary depressed at anthesis and enclosed by a rugose, verrucose nectary which persists in fruit as an obsolescent ridge around the ovary less than 1 mm. above the point of adnation to the hypanthium. Carpels follicular in fruit, slender and divergent throughout, prominently veined in the distal portion and along the styles. Styles slender, 1-2 mm. long, divergent 90° or recurved, stigmas capitate or more or less flattened. Seeds brown tuberculate, carinate along most of three sides, 1.0 mm. long, .45 mm. wide. (Fig. 3d, 13).

Chromosome number: n=28. (Fig. 2).

Habitat: moist, shaded cliffs, chiefly sandstone and quartzite.

Distribution in the U. S.: discontinuous, confined mostly to unglaciated areas—the Driftless Area of Illinois to Minnesota, and along the line of maximum extent of Pleistocene glaciation from s.w. Illinois to central Missouri. (Fig. 1.)

This species, which has often been confused with the *S. pensylvanica* complex, is held to be a distinct species on morphological characters, and also ecologic and distributional peculiarities. Furthermore, there appear to be no intergrading forms between it and any of the members of the *S. pensylvanica* group. The discontinuous range and specificity of habitat indicate a probable pre-glacial range of greater extent than at present, with little, if any, repopulation of the intervening areas, owing to destruction of habitat.

Specimens examined:—ILLINOIS: Jackson Co., May 9, 1873, ex coll. G. H. French, (USNM 44114); Jackson Co., May 9, 1873, G. H. French, plants 1, 2 and 3, (USNM 772168); Jackson Co., Makanda (type locality), May 5, 1900, C. F. Baker, (MBG 83868); Jackson Co., May 9, 1893, G. H. French, (UW); "so. Ill.," 1875, G. H. French, (USNM 44116, 44117); Ogle Co., Oregon, June 17, 1885, M. B. Waite, plant 1 only, (USNM 491007); Ogle Co., Oregon, Liberty Hill, July 11, 1905, ex herb. E. J. Hill, (UI); MISSOURI: Washington Co., Caledonia, June 25, 1936, J. A. Steyermark 11120, (MBG 1117289); Jefferson Co., May 8, 1896, H. Eggert, plant 2, (USNM 958397); Jefferson Co., May 23, 1882, H. Eggert, (USNM 1393994); Jefferson Co., May 11, 1887, H. Eggert, (MBG 83856); Jefferson Co.,

May 8, 1896, H. Eggert, (MBG 83861); Jefferson Co., near Pacific, May 30, 1928, J. H. Kellogg 1767, 1st sheet, (MBG 948955); Jefferson Co., *ibid*., 2nd sheet, (MBG 950628); Jefferson Co., Hog Hollow, May 30, 1928, J. H. Kellogg 15198, (MBG 1003894); Jefferson Co., Silica, May 1890, ex herb. F. Wislizenius 939, (MBG 84580); Jefferson Co., along Meramec riv., 1880, G. W. Letterman, (USNM 44111); St. Louis Co., Allenton, 1882, G. W. Letterman, (USNM 44113); St. Louis Co., Allenton, May 16, 1880, G. W. Letterman, (USNM 986370); St. Louis Co., Allenton Apr. 10, 1880, J. H. Kellogg, (USNM 1325414); St. Louis Co., Allenton, Apr. 16, 1880, G. W. Letterman, (MBG 775263); St. Louis Co., Allenton, June 20, 1880, Letterman, (MBG 772053); St. Louis Co., Meramec riv., Apr. 15, 1880, G. W. Letterman, (MBG 83858); St. Louis Co., St. Louis, May 1887, H. Eggert, (UM 178345); St. Louis Co., 1880, G. W. Letterman, (MBG 83818); St. Louis Co., Allenton, July 3, 1886, J. H. Kellogg (MBG 880983); St. Louis Co., Allenton, June 20, 1887, G. W. Letterman, (UI); St. Louis Co., Pacific, May 15, 1927, H. W. Edmonds, (MBG 1037095); St. Louis Co., along Meramec River 30 mi. from Mississippi River, Apr. 1880, G. W. Letterman (USNM 44112); St. Louis Co., St. Louis, May 11, 1887, H. Eggert, (UP 7438); St. Louis Co., St. Louis, May 11, 1887, ex

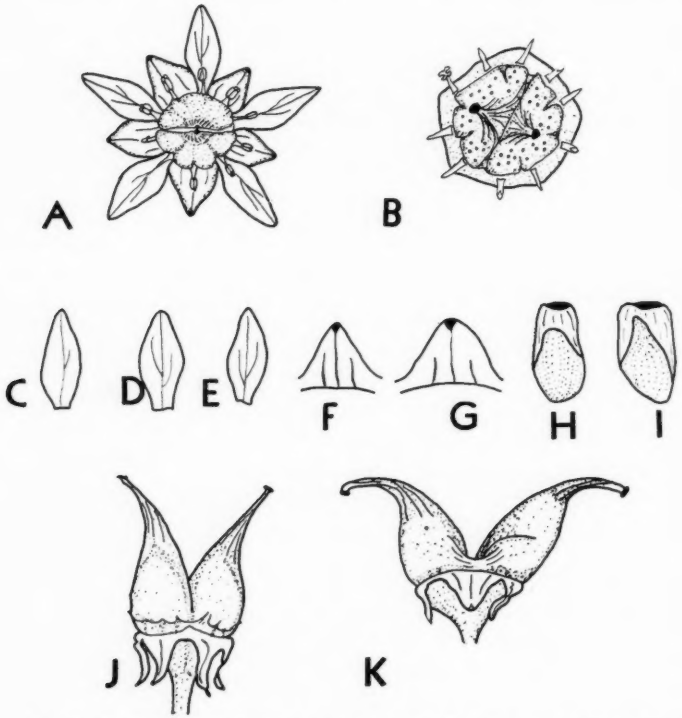

Fig. 13. *S. Forbesii:* A. flower at anthesis (×6); B. very young follicles (×6); C-E. petals (×6); F, G. sepals (×6); H, I. seeds (×20); J, K. mature follicles (×6).

herb. H. Eggert, (UP 7439); St. Charles Co., 2 mi. e. Femme Osage, Feb.! 23, 1931, J. A. Steyermark, (MBG 995439); Lincoln Co., Foley, May 25, 1933, J. A. Steyermark 8779, (MBG 1135617); Franklin Co., Pacific, May 8, 1896, H. Eggert, (USNM 754901); Warren Co., Warrenton, Apr. 19, 1931, J. A. Steyermark 568, (MBG 1027125); WISCONSIN: Iowa Co., Ridgeway, June 24, 1921, J. J. Davis, (UW); Iowa Co., Ridgeway, June 10, 1929, J. J. Davis, 2nd sheet, (UW); Sauk Co., Ableman, May 8, 1931, N. C. Fassett, H. V. Truman 12965, (UW); Vernon Co., Spring Coulee, Westby, June 16, 1932, H. P. Hansen 909, (UW); MINNESOTA: Winona Co., n.w. base Gwinn's Bluff, July 2, 1920, Rosendahl and Butters 3965, 2 sheets, (UM 178331, 178332).

11. S. Forbesii Vasey, f. bracteosa f. nov.

Bracteis inferioribus foliaciis, lanceolatis-ovatis, 5-9 cm. longis, 2-4 cm. latis.

Lower bracts foliaceous, lance-ovate, 5-9 cm. long, 2-4 cm. wide. Otherwise like *S. Forbesii.* (Fig. 3d).

Habitat: as for *S. Forbesii.*

Distribution in U. S.: as for *S. Forbesii.*

A single gene mutant, occurring occasionally with *S. Forbesii.*

Specimens examined:—MISSOURI: Jefferson Co., Silica, May 5, 1898, (MBG 83860); Jefferson Co., Silica, May 11, 1887, Eggert, (MBG 83862); St. Louis Co., Allenton, June 19, 1884, J. H. Kellogg (MBG 880982); St. Louis Co., Allenton, G. W. Letterman, (MBG 777205); St. Louis Co., Allenton, June 15, 1875, G. W. Letterman, (MBG 83820); St. Louis Co., June 20, 1884, G. W. Letterman, *type* (MBG 83859); WISCONSIN: Adams Co., Dell Prairie Twp., May 30, 1926, N. C. Fassett 3147, (UW); Vernon Co., Coon Valley, 1939, J. B. Marks, (UW); MINNESOTA: Winona Co., June, 1886, J. M. H. (UM 178375); Winona Co., n.w. base Gwinn's Bluff, May 3, 1925, C. O. Rosendahl, 4789, (UM 224438).

Summary

1. The polymorphism and confused status of *S. pensylvanica* L. are outlined, and the needs cited for determination of the factors causing such variation and for a new classification on the basis of those factors.

2. It is shown that polymorphism in *S. pensylvanica* has come about in three principal ways: (a) formation of distinctive intraspecific chromosome races through autopolyploidy; (b) hybridization between and within the intraspecific chromosome races; and (c) genic modification within such races. Experiments indicate that environmental influence acts as a factor of secondary importance, but is without taxonomic significance.

3. The gametic chromosome numbers 28, 42 and 56 are shown to occur in *S. pensylvanica,* rather than the single number n=29 reported in the literature.

4. Morphologic characters correlated with polploidy include: gigas characters, stoutness of scape, reduction in length-width ratio of leaves and floral parts, and larger seeds.

5. Geometric changes concomitant with polyploidy have been determined to be correlated with increase in cell size, and measurements of leaf epidermal

cell areas are found to be reliable indicators of the occurrence of polyploidy where material for chromosome counts is not available.

6. Such differences in cell size, and in leaf shape, with polyploidy, are shown to be statistically significant.

7. It is suggested that var. *purpuripetala* has been derived recently from ssp. *eupensylvanica* by simple genic differentiation alone, whereas *S. Forbesii*, which may be either ancestral or derived, is probably considerably older as its confinement to unglaciated areas indicates.

8. A new and more natural classification is here proposed, based on cytological and morphological characters which are shown to be taxonomically reliable.

ACKNOWLEDGEMENT

The author expresses appreciation to Dr. C. O. Rosendahl and Dr. F. K. Butters for their helpful counsel and guidance during the progress of this study, to the curators of the various herbaria from which loans of specimens were made, and to the many others who were of assistance in field collections of material.

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Observations of Three Species of Silpha (Coleoptera: Silphidae)[1]

A. C. Cole, Jr.

On April 19, 1941, carcasses of two freshly killed short-haired dogs were obtained at Knoxville, Tennessee. With a scalpel the entire length of the abdominal cavity of one carcass (No. 1) was opened, so that the viscera were exposed. The carcass was placed in an open area within the border of a woods. The other carcass (No. 2) was left intact, and was put beside a ledge of rocks on a grassy hillslope. The two locations were in the same general area and about a quarter of a mile apart. Each carcass was anchored firmly to the soil with strands of heavy wire fastened to buried pegs. The carcass in the woods was at least partially shaded most of the time, while that on the hillslope was exposed to direct sunlight at almost all times. The weather between April 19 and April 27 was rainy and cool, while that subsequent to April 27 was warm and bright. May especially was very dry.

It seems desirable to compare the insect activity on the two carcasses for each successive date of examination rather than to arrange a sequence of observations of one carcass and then that of the other.

On the day following deposition of the carcasses a visit was made to both locations. There were no silphids present, nor was there any evidence of activity of other insects. On April 21, many mating pairs of *Silpha inaequalis* were observed on carcass No. 2, and dipterous maggots were abundant in the decomposing flesh. The odor of tissue putrefaction was strong. Carcass No. 1 showed no evidence of dipterous maggots, and no silphids were observed.

Many mating pairs of *S. inaequalis* were still present on carcass No. 2 on April 24, and a large number of mating pairs of *S. noveboracensis* was observed for the first time. A single adult female of *S. americana* was on the carcass. Dipterous maggots were present in enormous numbers, and several adults of a large staphylinid *(Creophilus villosus)* were running over the carcass. On the same date, mating pairs of *S. noveboracensis* were very numerous on carcass No. 1. Only a few mating pairs of *S. inaequalis* were present. Dipterous maggots were abundant, and many adults of the large staphylinid were running upon the carcass.

On April 28, mating pairs of *S. inaequalis* were very scarce on carcass No. 1, and the number of adults of *S. noveboracensis* had been reduced materially. Maggots were still abundant in the carcass, but the odor of decomposition was noticeably less than on the previous visit, although the carcass was still very

1 Contribution no. 2, Department of Zoology and Entomology, University of Tennessee, Knoxville.

moist. No silphid larvae were found. By this date, carcass No. 2 had dried materially. Around the periphery of the carcass were found for the first time a few small larvae of *S. inaequalis*. These larvae moved rather slowly when disturbed, and crawled beneath the carcass. Twelve mating pairs of *S. americana* were observed inside and beneath the hind quarters of the carcass which consisted of rather soft skin, strips of dried flesh, hair and bones. Maggots, although still abundant, were less numerous than on April 24, a large number of them having left the carcass and pupated in the adjoining soil.

Small larvae of *S. noveboracensis* were abundant on and beneath carcass No. 1, on April 30. Also present were several larvae of *S. inaequalis*, most of which were running about in bright sunlight (at 2 p.m.)—on the carcass, the hair, in adjacent debris and on logs. There was no evidence of larvae of *S. americana*. Maggots were rather few; most of them had already pupated. Adults of the large staphylinid were numerous in and beneath the carcass. A few mating pairs of *S. noveboracensis* and *S. americana*, but none of *S. inaequalis*, were observed. The carcass was very dry; only hide, hair, bones and dry strips of flesh remained. Silphid larvae were more common on carcass No. 2 on April 30 than on April 28. All, however, were still in the early instars. A number of mating pairs of *S. noveboracensis* was found, but no adults of the other two species were observed. Maggots still worked in what soft decomposed flesh remained. Dermestid adults were in the mats of hair, and adult histerids crawled upon the hide. Several adults of the large staphylinid were observed within the carcass.

On May 4, several young larvae of *S. americana* were found in and on carcass No. 1. Larvae of *S. noveboracensis* and *inaequalis* were quite scarce. Many adults of the large staphylinid were evident. The carcass was very dry, and no maggots were found. A few fully grown larvae of *S. inaequalis* were seen on May 4 on and in carcass No. 2. Nine single females of *S. noveboracensis* were on the carcass, which was still somewhat moist. Maggots were absent. Many adult dermestids were on the hide and hair. A few mating pairs of *Trox* spp. rested motionless on the hair-matted hide.

Several small larvae of *S. americana* were in the dry hind quarters of carcass No. 1, on May 12, and several half-grown as well as a few full-grown larvae of *S. noveboracensis* were in and beneath the carcass. Larvae of *S. americana* move very swiftly, while those of *S. noveboracensis* move much more slowly and when disturbed "feign death" by bringing the anterior and posterior ends of the body together ventrally. Numerous young dermestid larvae were on the hide and in the hair.

On May 16, populations were much the same on both carcasses as those of May 12. On May 24, several larvae of *S. noveboracensis* and a few of *S. americana* were still feeding in the hind quarters of carcass No. 1. Mating pairs of *Trox* were abundant; twenty-eight adults, representing three species, were collected from the hide and hair. A few full-grown larvae of *S. noveboracensis* were found in a mat of hair which, together with the bones and hide, were all that remained of the carcass. No silphid larvae were observed on May 30 on

the remains of either carcass. The soil beneath the carcasses contained several larvae of the large staphylinid as well as a number of histerid larvae.

The following conclusions are evident:

1. The intact carcass exhibited earlier evidence of insect activity than did the incised carcass.

2. Mating pairs of *Silpha* spp. made their appearance on the carcasses two to five days subsequent to the death of the animals. Attrahent properties of the carcasses were apparent from the dates of the initial appearance of the silphid adults until April 30—a period of seven to ten days.

3. Silphid larvae were first observed seven days following the appearance of the adults on the carcasses. Larvae were associated with the carcasses three to four weeks after the date of the first ones observed. Since eggs are deposited by the females over a period of several days, different instars of a single species were found concurrently at the carcasses.

4. Larvae of *S. noveboracensis* predominated on the carcass in the woods, while those of *S. inaequalis* were more numerous on the carcass on the hillslope. There is some indication, therefore, that adults of *S. inaequalis* are more greatly attracted to carrion in exposed situations than to that in shaded ones. Also, there is evidence that both situations attract adults of *S. americana* to approximately the same degree.

5. Larvae of *S. inaequalis* were observed feeding upon the carcasses and crawling upon adjoining objects while they were exposed directly to the rays of the sun. This tolerance of the larvae, and also of the adults, lends strength to the evidence that the habitat on the unshaded hillslope was perhaps more attractive to adults of *S. inaequalis* than to those of *S. noveboracensis*. Dorsey,[2] in his paper on silphid larvae, to which the reader is referred for a taxonomic and biologic study, records his observations of the larvae's not being tolerant to the force of the sun's rays. These observations, although conflicting with those of the writer, serve to emphasize the variability of behavior of silphids. Factors other than light may be responsible for stimulating the activity of the larvae in one locality or another.

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2 Dorsey, C. K., "A comparative study of the larvae of six species of Silpha (Coleoptera, Silphidae)," Ann. Ent. Soc. Amer. **33**:120-139. 1940.

Herpetological Fauna of Jackson and Union Counties, Illinois[1]

Fred R. Cagle

This survey represents the results of several years haphazard study in southern Illinois and two years intensive, organized research in Jackson and Union counties. This area, with its moderate climate, diversified topography and vegetation, and central location, provides suitable habitats for a wide variety of reptiles and amphibians. Information on the bionomics of many of these species is scant and few data are available on the systematic position of some of the subspecies. This report contributes additional data on the herpetofauna of this region.

I am indebted to Dr. H. K. Gloyd, Chicago Academy of Sciences; Dr. K. P. Schmidt, Field Museum; Miss Doris M. Cochran, National Museum; Dr. Charles Bogert, American Museum of Natural History; and Mrs. Helen T. Gaige, Michigan Museum of Zoology for lists of specimens deposited in their respective collections. I am further indebted to Dr. Gloyd, Dr. Schmidt, Mrs. Helen T. Gaige, Mr. William Stickel, Dr. Norman Hartweg, Dr. Joseph Bailey for their aid in identification of specimens and to Dr. Edward E. Hall, Southern Illinois Normal University for permission to quote sections and reproduce illustrations from the book, "Geography of the Interior Low Plateau and Associated Lowlands of Southern Illinois."

Much information has been contributed by Mr. R. Marlin Perkins, Director, Buffalo Zoological Gardens; Dr. Carl E. Gower, Michigan Department of Conservation; Mr. Philip E. Smith, University of Illinois; Dr. David Thompson, Illinois Natural History Survey; Dr. Hugh Clark, Des Moines Still College of Osteopathy and Mr. Norman Meinkoth, University of Illinois.

I am grateful to the many students and colleagues who have aided in the field work and particularly to Mr. Lendell Cockrum for his enthusiastic participation in both field and laboratory work.

Finally, I wish to express my sincere gratitude to Miss Hilda Stein, Zoology Department, Southern Illinois Normal University, who stimulated the writer to begin this study.

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Geology and Physiography

Jackson and Union counties lie in southern Illinois between the meridians 80° 10′ and 89° 45′ west and the parallels 37° 15′ and 38° 0′ north. Their total area includes approximately 916 square miles and has a maximum length of 63 miles and a maximum width of 28 miles (Fig. 1).

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1 Contribution No. 6 from Museum of Natural and Social Sciences, Southern Illinois Normal University, Carbondale, Illinois. The completion of this research was made possible by grants from the Illinois Academy of Sciences.

The area includes portions of two physiographic provinces of the United States; namely till plains and dissected plateaus. The characteristics of these two sections respectively are summarized by Fenneman (1931) as "young till plains; morainic topography rare; no lakes" and as a "low maturely dissected plateau with silt filled valleys." The two counties may be divided into three roughly delimited topographic units: The Mississippi floodplain; a rough, dissected upland; and a rolling lowland (Fig. 1).

The Mississippi flood plain is five to seven miles wide and 330 to 365 feet above sea level. Its flat surface is seamed by numerous abandoned river channels that with the exception of those that have been drained form perennial swamps. Several drainage ditches have been constructed to drain the bottom lands (Fig. 1).

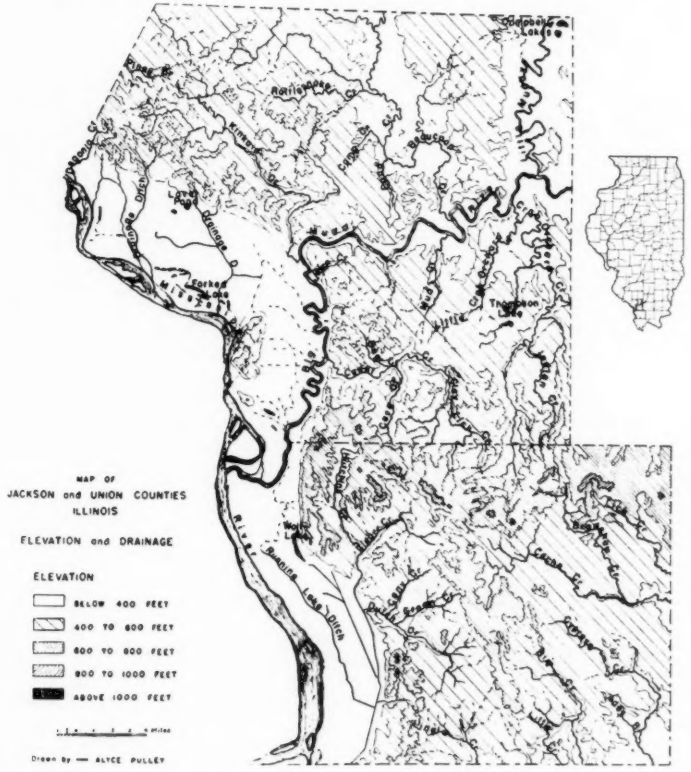


Fig. 1. Topography map of Jackson and Union Counties taken from United States Topography maps.

The flood plain lakes are shallow and have wide borders of thick swamp growth. They fluctuate a great deal in level and the smaller ones go dry during drought seasons. Wolf Lake, the largest of the flood plain lakes, is an elongate, shallow body of water flanked by the Mississippi bluffs on one side, a railroad on the other and terminating in extensive swamps which support an unusually rich herpetofauna (Fig. 3).

The soils of the flood plain have a high percent of clay and form a rich alluvium that produces most of the grain crop of the region. In the non-cultivated portions this soil supports a dense cover of vegetation.

In southern Union county the bottomlands are dominated by Cypress trees associated with the Tupelo and Red and Black Gums. In the same situation on other sections of the floodplain the Pecan, Water Hickory, Sycamore, Ash, Elm, Hackberry, Honey Locust, Cottonwood and water-tolerating oaks also grow. The cypress forests are the northernmost in western Illinois.

The flood plain is bordered by high, almost continuous bluffs and rocky hillsides broken frequently by steep, rugged ravines 100 to 300 feet deep (Fig. 1). This deeply dissected bluff area becomes less rugged to the east where the topography is more rolling. This rough, dissected upland extends from the northwestern corner of Jackson county southward along the river to a point south of Carbondale and thence completely across southern Jackson and Union counties. This area is a portion of a high ridge, commonly called the Illinois Ozarks, extending across southern Illinois.

In Jackson county this section is chiefly underlain by Pennsylvanian sandstone; in Union county the topography is dominated by bedrock of Mississippian and Devonian periods. The Devonian limestone forms the blufflands along the Mississippi valley and the Mississippian rocks the less rough areas eastward.

The part of this section just south of Carbondale is underlain by the shales and massive sandstones of the Pottsville formation. The latter layers are 40-170 feet thick and give rise to a rough and rugged topography with numerous bluffs and cliffs. The lower members form a bold scarp, locally called the Pottsville scarp, extending across northern Union county. South of the scarp the topography is similar but in some places gently rolling. In places the Pottsville sandstone has protected underlying beds from erosion and resulted in the formation of high isolated hills or knobs.

Lamar (1925) states, "Although the relief of the rough belt of country which crosses southern Illinois in an east-west direction through Union, Johnson, Pope, and Hardin counties, is not as great as that of the Ozark Highlands in Missouri, it seems reasonable to consider this rough belt as a continuation or spur of these highlands."

The soils of this dissected upland region or "Ozark Ridge" were developed from loess that accumulated after the glaciation of the northern section. The southern limit of glaciation is just south of Carbondale.

The trees of the hilltops and hillsides are primarily oak and hickory. Beech forests have developed in the bottoms of the valleys and along the sides of ravines where cherty and gravelly soils suitable for their growth occur. Much of the area is covered with bush and sparse forest growth.

This entire region supports a rich herpetofauna. The bluffs along the Mississippi have many dens at their bases where large numbers of snakes congregate during early spring and late fall. These dens are annually visited by groups of snake hunters who frequently destroy large numbers. One group

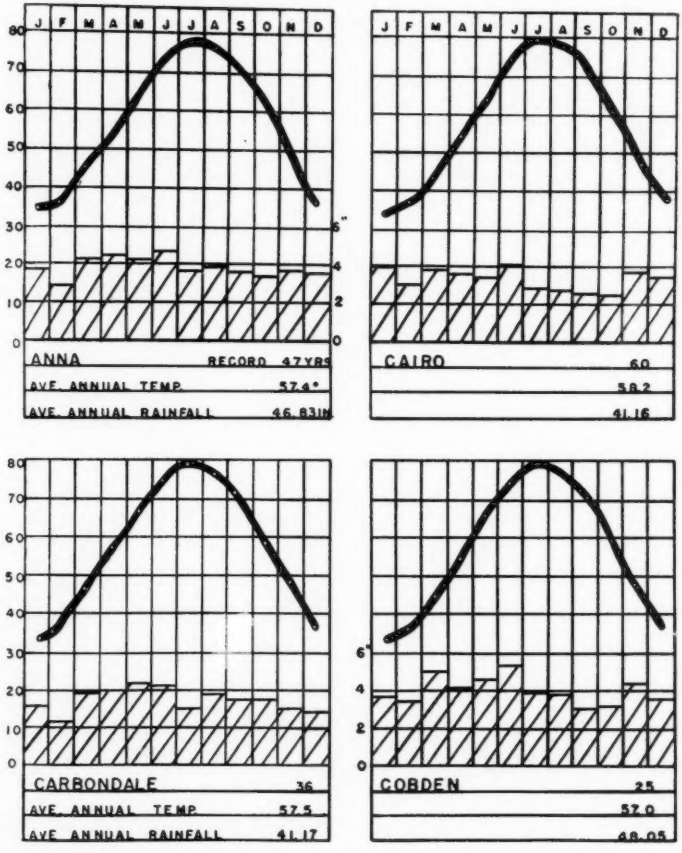


Fig. 2. Climate charts prepared by Hall, 1939 from data of weather stations within or adjacent to the area described.

shot 57 snakes in a two hour period during September, 1940. The majority of these were pilot black snakes.

For several years these dens provided an abundant supply of snakes for the St. Louis Zoological Gardens. Mr. R. M. Perkins, Director, Buffalo Zoological Gardens and formerly Curator of Reptiles, St. Louis Zoological Gardens states in correspondence that during the years 1928-29-30 these dens were alive with snakes and that the collectors took many hundreds. During the past few years the activities of cattle and hogs and the regular shooting of snakes by hunters has greatly depleted the population and a day's collecting should be now considered successful if 15 or 20 snakes are taken.

The third topographic unit is a gently rolling lowland in northeastern Jackson county (Fig. 1). It is broken here and there by hills capped with resistant sandstone but the elevation is principally below 400 feet. The eastern section is covered by an extensive swamp area that remains wet throughout much of the year but occasionally goes dry except for a few ponds and lakes. The several small lakes support a luxuriant fauna and flora.

The area immediately north and east of Carbondale is very flat and is for the most part open grasslands with scattered patches of oak-hickory forest.

The soils are typically flood plain except for a section of prairie soils where the original prairie extended southward into Jackson county.

This unit supports a slightly different herpetofauna than the other two areas.

The physiography of these counties may be better understood after a brief survey of the recent geologic history of the two counties. Southern Illinois was exposed to the same forces that formed the Missouri Ozarks. Most of Union county and the southern part of Jackson county were included in this uplift and a subsequent, prolonged period of erosion formed the rough, hilly terrain in this region.

During the Glacial epoch this erosion was alternately slowed and intensified as the climates changed. Only one of the great glaciers, the Illinoian, entered Jackson or Union county, and it covered only the northern third of Jackson county. This region was thus leveled off to some extent and this action combined with resulting deposition explains the much smoother relief in northern Jackson county.

As the glacier melted and retreated, loess accumulated on the surface of the glacial drift. This loess varies from a thickness of four feet in the northeastern part of Jackson county to a maximum of fifty feet or more on the Mississippi bluffs.

During the close of the glacial epoch the large masses of water from the melting glaciers in central and northern Illinois carried huge quantities of sediment that dammed the outlet to tributary streams. One such blockade caused the formation of a large shallow lake, now extinct, that extended over

Fig. 3.—Wolf lake, a flood plain lake in Union County, supports a wealth of aquatic plants and rich herpetological fauna. Fig. 4.—A rocky creek bed illustrative of the type found in western Union County.

a large area to the north and east of Carbondale and Murphysboro. Sediment carried from higher ground gradually filled this lake. The previous glaciation and presence of this lake explains the origin of the broad, flat, poorly drained lands in that area.

Streams have since cut new valleys through this flat low upland, but it is still inadequately drained.

Drainage

Jackson county is principally drained by Big Muddy River, the largest stream (Fig. 1). Its main tributaries are Crab Orchard Creek, Little Muddy River, Beaucoup Creek, Kinkaid, Cedar, Indian and Drury Creeks. The channels of the streams are very crooked and the bottomland is frequently flooded. The valleys vary from a quarter of a mile to two miles in width and are for the most part wooded and covered with bush.

Western Union county is drained by Cedar Creek and its tributaries. Unlike those of the Big Muddy systems these streams have straight channels and extensive length of rock bottom (Fig. 4).

Eastern Union county is drained by tributaries of the Cache river that flows westward along the southern border of Union county and thence southward to the Ohio. The Union county tributaries of the Cache overflow because of their crooked channels and insufficient river outlets. The bottom lands are swampy.

The volume of water carried by all the streams varies greatly with the season. In the summer the water level may be so low that most of the streams may be easily crossed in many places and the water in the tributaries is correspondingly low. After a period of rainy weather the creeks become very swollen and backwater covers large areas of the flood plains.

Climate

The climate is typical of that prevailing in north-central United States. Hall (1940) describes the climate of southern Illinois: "It has hot summers, averaging near 80 degrees for July and cool winters, averaging near the freezing point for January. It is in the northern border of the hot summer and cool winter temperature region as defined by Parkins. The absolute yearly range of temperature is around 100 degrees. The absolute maximum temperature for the region is 113 degrees and the absolute minimum temperature is -24 degrees; both were recorded at the Carbondale station. This range is enough to give a very invigorating climate. One of the well-traveled paths of the lows cross southern Illinois in winter bringing changeable weather. It is not uncommon for the temperature in winter to drop 40 to 50 degrees in only a few hours. Warm south winds and sunny skies suddenly give way to cloudy skies, rain and snow, followed by clear cold weather. The highs bring in weather of zero and below quite frequently. In the summer the paths of the lows have moved much farther northward and the hot dry sub-tropical winds from the south blow across the region. These winds are dry because they have lost much of

their moisture in southern United States immediately after coming on to the land. However, frequent thunder showers give rainfall to the region even in summer. The average number of thunder showers per year at Carbondale over a 17-year period was thirty-three. Continued high temperature with little rainfall during many of the summers cause frequent droughts. Thirty-six days of one hundred degrees or over were recorded during the drought of 1936 at Carbondale. The average rainfall for many years shows a fairly even distribution throughout the year with a trend toward a late spring and early summer maximum." The four charts in Fig. 2 present further data on climatic conditions as recorded at four weather stations within or adjacent to the two counties.

Previous Investigations

Davis and Rice (1883) suggested that 30 amphibians and 71 reptiles occurred in the southern part of Illinois. Their report was based on "well authenticated specimens" now unavailable and local lists compiled by Mr. Robert Ridgeway, Dr. P. R. Hoy, Prof. E. Stein and Dr. Schenck.

Garman (1892) listed 40 forms of amphibians and 80 forms of reptiles from the state. Since Garman no studies of the complete herpetological fauna have been published but the turtles of the state were described by Cahn (1937) who listed eleven species and subspecies of turtles from Jackson and Union counties.

Methods

The survey work was divided into three phases; field work to collect and observe, laboratory work to check and elaborate field studies, and study of museum specimens. The last phase of the work has been confined to material deposited at the Southern Illinois Normal University. Specimens listed from other institutions have not been examined by the author.

Field work was continued through each month of the year although work was most intensive through the spring and summer months. Collecting crews were rarely less than three persons, usually the writer and two student assistants skilled in collecting. All important observations were carefully checked in the field and any important specimens preserved for deposit in the museum collections.

No attempt has been made to include detailed field notes or routine observations of no known significance as such a procedure would only result in undue bulkiness. The author has attempted to select the important sections of data for detailed presentation and to summarize whenever possible.

List of Species

1. *Necturus maculosus* (Rafinesque).—This species is common in the Big Muddy River, Crab Orchard Creek and the Mississippi river.

Jesse Grammer, an employee of the power plant at Grand Tower, reported that they were frequently observed in abundance about the water inlet to the

plant. They are sometimes taken on hook in the Mississippi and the Big Muddy rivers.

The adults move into the shallow sloughs and backwaters during May to spawn. Eggs were collected in May, 1939, from the underside of a rotten log in a slough near Ware. A collecting trip to this same area, June 3, 1939, yielded only one larva 10 cm. long despite energetic seining and hand collecting. S.I.N.U.—49, 216.

2. *Cryptobranchus alleganiensis* (Daudin).—Several specimens of the Hellbender have been reported from the Big Muddy and the Mississippi rivers. Locally they are called "Devil Dogs."

Davis and Rice (1883) stated that this species was found in the Mississippi and its tributaries, but as yet no specimens from Illinois have been deposited in museum collections.

3. *Triturus viridescens louisianensis* (Wolterstorff).—Specimens have been collected near Anna, Alto Pass and in the Campbell Swamps east of Elkville. Mrs. Josephine Cagle collected a specimen from a decaying log in the Campbell Swamps Sept. 5, 1938.

Mr. Philip Smith reports that this species is rather abundant in the vicinity of Herrin. In December, 1939, he observed a large number of *Triturus* and *Siren* in a culvert connecting two ponds. Cagle and Smith (1939) described this aggregation in detail.

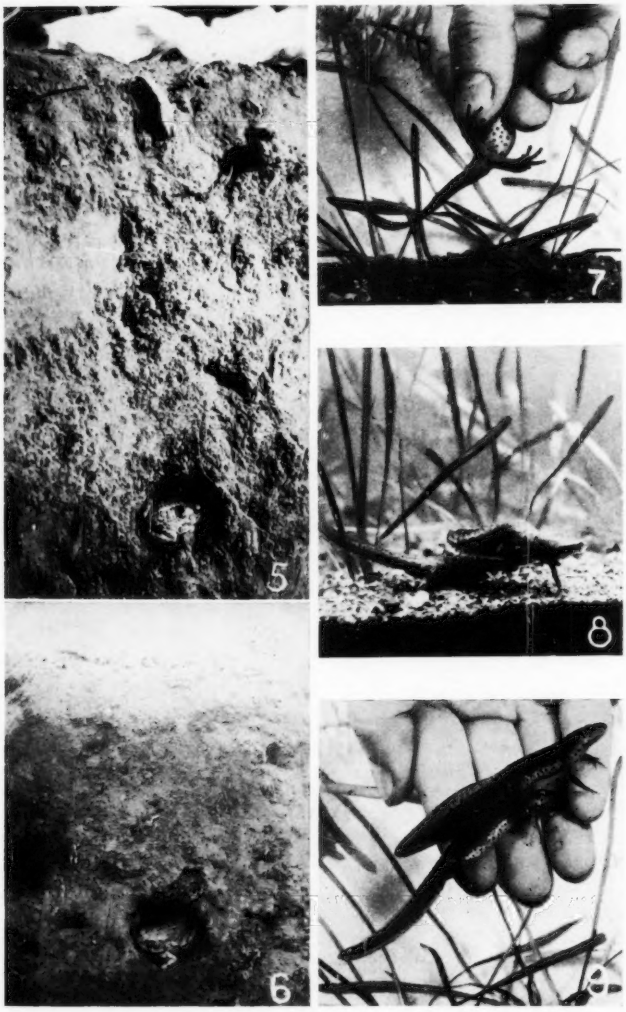
Triturus from this collection retained in an aquarium actively continued courtship for several days but no eggs or spermatophores were deposited. The male would stealthily approach the female, settle over her and clasp her securely with the hind legs (Fig. 7, 8, 9). The tail was frequently bent far forward to stroke the side of the female's head (Fig. 8). On several occasions the female attempted to escape and the male secured a hold about the head or anterior part of the body. The males were aggressive and resisted attempts to separate them from the females. One male was observed to retain a hold on a female for 24 hours.

Several pairs were observed in courtship in a shallow pool near Anna, Illinois, February 28, 1939. Eggs were collected a few days later from the same pool. A.M.N.H.—23277-79; F.M.N.H.—11745; S.I.N.U.—142, 152, 159, 123, 141.

4. *Ambystoma jeffersonianum* (Green).—Rare in this region. C.A.S.—2511, 381.

5. *Ambystoma maculatum* (Shaw).—This species is abundant in the low, wet oak-hickory forests adjacent to creeks and swamps. They were most frequently collected deep in the interior of decayed logs.

A specimen collected in Indian Creek Valley near Carbondale, Illinois, October 25, 1939, was concealed in a cavity eight inches within a large log. The cavity had apparently been frequently used by the salamander as the moist,



Figs. 5, 6.—Toads buried under the surface. In Fig. 5 close observation indicates the filling of the original tunnel lead to the cavity. Fig. 7.—The specialized clasping structures in the male newt. Fig. 8, 9.—Courtship behavior in the newt.

decayed wood was pressed and worn to form a neat chamber with an aperture leading out at the ground level.

Although this species is usually found in abundance in the proper habitat, no other individuals were found in this area but numerous specimens of *Plethodon glutinosus* were collected. *Ambystoma talpoideum* had been collected there previously.

When examined in the laboratory, this specimen's stomach contained two large centipedes and one snail. The body cavity was crowded with fat.

A single individual collected in the water several feet from the shore of Thompson Lake on the night of May 8, 1939, was an unexpected collection as it had been assumed that this species rarely ventured into the water except during the breeding season.

Many clusters of eggs were observed in shallow pools in a swampy oak-hickory forest between Black ditch and Grassy lake west of Anna, April 14, 1940. The pools were nowhere more than one foot deep and were scattered through several acres of forest. A thick bed of dead leaves formed the bottoms of the pools and numerous fallen branches cluttered the area. The eggs were embedded in a firm gelatinous mass attached to the broken twigs and branches. Several hundred clusters of eggs were observed in a few pools and many more were doubtless present in others. The eggs were all in a similar stage of development and larvae squirmed from some of the masses when they were disturbed.

The egg masses were covered with a brown membrane-like coating of diatoms that made them almost invisible against the leaf-covered bottoms of the pools. When the masses were examined in the laboratory, they appeared light green in color. Further examination indicated the presence of a green algae. At the suggestion of Dr. W. Welch, Botany Dept., S.I.N.U., eggs were shipped to Dr. Gilbert M. Smith who identified the algae as *Oophila amblystomae* Lambert. F.M.N.H.—11763, 18591; C.A.S.—230-244; S.I.N.U. —164, 242, 253, 226, 237, 241, 91.

6. *Ambystoma opacum* (Gravenhorst).—This species was collected from the low oak-hickory forests throughout the area, but was never collected in abundance in any one locality. A collection of ten or fifteen specimens represented the results of a hard day's collecting in the best habitat worked. Although specimens were most often observed under moist, decaying logs or wet rocks partially buried in the ground, many were collected from quite dry situations. Such specimens had a smooth, dry skin and were apparently well adapted to the dry surroundings.

On March 2, 1939, several specimens were collected from under sandstone slabs in the mouth of a cave 50 feet above the floor of Indian Creek Valley. The rocks were partially buried in the clay soil and had obviously not been disturbed for a long period. The salamanders were found in shallow, oval

cavities under the rocks and adjacent to the edge. One under a rock sixteen inches in diameter and six inches thick had formed a neat cavity that had apparently been used as a winter retreat. The cavity was one inch below the ground and had a well-defined entrance that led at an angle to the surface. This entrance was 3/16 inch high by 1/2 inch wide and was worn smooth. The exit was covered with leaves and other debris.

No observations were made on the reproductive habits of this species. O'Donnell (1937) stated that eggs were laid during October and November in southern Illinois. A.M.N.H.—11853-54; F.M.N.H.—11744, 11765, 13207, 18578, 18579, 18580; C.A.S.—245-251, 2000-2001; S.I.N.U.—52, 163, 35, 76, 168, 266, 248.

7. *Ambystoma talpoideum* (Holbrook).—Collections have been made at only one point, Indian Creek Valley, southwest of Carbondale. The Chicago Academy of Science has a specimen from Anna and another one from six miles southwest of Jonesboro. This region is the northernmost limit of its range. C.A.S.—2512, 2002, 2023; S.I.N.U.—251.

8. *Ambystoma texanum* (Matthes).—This salamander occurs most abundantly in the woodlands adjacent to creeks and rivers, but is sometimes collected in gardens and open fields.

The adults emerge from hibernation with the first warm rain of late winter and move to the shallow pools, ponds and streams to breed. Five large females were collected from pools in an oak-hickory forest three miles north of Carbondale, February 3, 1939. A heavy rain had fallen the night before and the temperature of the water in the pools was 6.8° centigrade. The salamanders were sluggish but had successfully performed courtship as indicated by the presence of numerous egg clusters.

One of the females was placed in an aquarium where she laid many eggs the night collected. A count of these eggs and the ones left in the body cavity indicated that this individual could have deposited 550 eggs. As the eggs average 4.6 to a cluster, it is apparent that one specimen may deposit many egg clusters.

Soon after this collection was made these pools were frozen, but larvae in abundance were collected there during the last of March.

Mr. Philip Smith reported observing this species breeding near Herrin, February 10, 1939. This was the evening of the first warm rain in that vicinity.

Numerous egg clusters were observed in pools near the Carbondale City Reservoir and in small temporary streams near Murphysboro, March 15, 1939. The pools were examined May 19 and large numbers of mature *texanum* larvae were collected. Several that had lost practically all trace of gills were collected from under logs near the water. *Pseudacris* and *Rana* tadpoles were abundant in the same pools.

Numerous spermatophores and egg clusters were observed in a shallow

elbow slough near Crab Orchard Creek, two miles west of Carbondale, March 17, 1940. No salamander could be found despite a careful search of the vicinity but on a return trip the same evening five (four females and one male) were collected under logs at the edge of the water. The females had all deposited their eggs.

Egg clusters and spermatophores were distributed over a large part of the shallow slough. In order that an approximation of the total number of egg clusters and eggs could be made, the collectors selected a section at random and marked off two strips across the stream. Each strip was 42′ 6″ long and 7′ wide. A collector counted the eggs in each strip by wading into the water and carefully examining and then casting aside every piece of debris that might carry a cluster. As the eggs were in advanced stages of division the fertile eggs could be easily separated from the infertile. The number of fertile and infertile eggs in each cluster was recorded. This method gave a rather accurate indication of the total number of clusters and the precentage of viable eggs.

In the first strip 60 clusters were found. Maximum number of eggs per cluster was eight; minimum number was one. In the second strip 61 clusters were found. Maximum number of eggs per cluster was nine; minimum number was one.

The area in which egg clusters could be observed was 125 feet. If the clusters were well distributed through this area, as they appeared to be, there were approximately 1071 clusters in the area.

During this trip four males were collected from under logs in the edge of the water. All stomachs were packed with aquatic earthworms.

This species has been frequently reported by W.P.A. excavation crews that find them at the bottom of crayfish burrows. At least 10-15 specimens were thus collected by one crew digging a drainage ditch east of Duquoin.

Mr. Philip Smith of Herrin dug a specimen from the bottom of a crayfish hole three feet deep, December, 1938.

These records indicate that this species spends the winter deep in the subterranean retreats prepared by the crayfish. U.S.N.M.—93203; F.M.N.H. —11764, 18594, 18595, 18608; S.I.N.U.—199, 200, 264, 288, 125, 231, 245, 289, 263, 254, 107, 118, 197.

9. *Ambystoma tigrinum* (Green).—This species is common throughout the area. It has been frequently collected in the immediate vicinity of homes. S.I.N.U.—56, 234, 236, 242; F.M.N.H.—18625.

10. *Plethodon cinereus* (Green).—This species was collected in only two localities within the area. Two specimens were taken in the mixed oak- hickory-beech forest in the valley of the Big Muddy River near Murphysboro, Illinois, and numerous specimens near Wolf Lake in Union county. S.I.N.U.—290; F.M.N.H.—18597-18602; C.A.S.—2509-10, 2024-2029.

11. *Plethodon glutinosus* (Green).—Members of this species have been

collected in abundance from the margins of cypress swamps, the low oak-hickory forests bordering the creeks and swamps and the beech-maple forests of the rocky ravines of the Mississippi bluffs. The largest collections were made in Indian Creek Valley, 5 miles south of Carbondale, where specimens were taken by splitting the large, decaying logs scattered over the creek valley. One such log 18 inches thick and 114 inches long yielded 10 salamanders most of which were found in the galleries excavated by the Passalus beetle.

In areas where such retreats are not readily available the salamanders find protection under any available material. Thus many specimens were collected on several occasions from under large slabs of sandstone or from under the layers of decaying moist leaves on the forest floor.

Specimens were collected from a cave in Rattlesnake canyon on two occasions. Ten small juveniles were collected from the matted debris on the floor in the twilight zone of the cave and one large female from under a 6″ slab of rock 20′ within the entrance of the cave, September 19, 1938.

Numerous field observations indicate that this species moves freely about at night foraging for food but retreats to dark moist places during the day. Very active specimens were often observed at night in dry places where they were rarely seen during the day, and night examinations of decayed logs yielded comparatively few salamanders.

There is also a distinct seasonal movement of the members of this species. During spring and early summer they may be found in abundance under rocks and leaf mold high on the rocky slopes of the creek valleys. As late summer approaches they move down the slopes to the more moist areas or aggregate close against the cliff walls where there is an abundance of moisture. During late summer and early fall these slopes are barren of salamanders, but they are abundant within the moist interior of partially decayed logs on the valley floors.

One of the wooded slopes where salamanders had been observed to be abundant was burned over by ground fire that destroyed all forest floor vegetation April 1, 1937. The area was examined carefully one day after the fire. An area 100 feet square was selected and every rock and log examined for living or dead salamanders. No dead or injured ones were found, but three unharmed ones were collected under rocks partially buried in the debris.

Few observations were made on the breeding habits of this species. A large female collected near Chalk Bluff, March 15, 1939, contained eggs ready to be deposited.

Forty-three specimens collected in Indian Creek Valley Oct. 22-25, 1939, furnish some interesting suggestions on growth rates in this species. These 43 individuals were drowned, preserved in 10% formalin and the total length, tail length, and body length taken with vernier calipers. The largest specimen was a female measuring 14.82 cm. in total length; the largest male was 13.94 cm. The smallest specimen measured 6.02 cm. Size distribution was as follows:

Females		Males	
6.02	11.69	10.65	6.29
6.54	12.00	11.09	6.80
7.11	12.05	11.14	7.86
9.21	12.20	12.38	8.65
9.59	12.74	13.20	10.08
10.77	13.18	13.94	10.29
10.83	14.15		
10.85	14.40		
10.90	14.78		
11.35	14.82		

Measurements of 6 ♂'s and 5 ♀'s were omitted because of injury to the specimen.

Three collectors worked a section of the valley carefully for these specimens and were particularly careful to watch for the very small specimens. F.M.N.H. —13208, 13209, 13210, 18596, 18609, 18610, 18611, 18612, 23714; C.A.S.—256-261, 2010; S.I.N.U.—33, 174, 201, 233, 267, 51, 137, 155, 177, 197, 143, 196, 258.

12. *Eurycea longicauda longicauda* (Green). — Abundant in the creek valleys of the bluff region where it lives under the rocks and logs near the edge of the water, but occasionally collected from within logs adjacent to the creeks of eastern Union county. When the shallow streams are dry, the salamanders move to the moist center of decaying logs or to wet crevices in the rock cliffs.

In May, 1926, two hundred specimens were collected in a few hours from the rock strewn floor of a canyon near Murphysboro. Although *Eurycea* had never been collected in abundance there and subsequent collections have been meager, specimens were amazingly plentiful and most of the larger rocks about the edges of the shallow rock-bottomed stream concealed one or more salamanders that invariably fled into the water when disturbed. There was no evidence of breeding activity nor were any other special conditions observed that might account for the sudden abundance.

Twenty-eight stomachs taken from these salamanders contained large numbers of spiders, the most important food item, and small numbers of hemiptera and pill bugs. F.M.N.H.—13211, 13212, 13213, 18590, 23709, 23710, 23711(33), 23708; C.A.S.—2508, 1999; S.I.N.U.—139, 145, 157, 246, 175.

13. *Eurycea lucifuga* Rafinesque.—Common in and about the mouths of caves. Mr. Carl Gower reported it as abundant in Kinkaid Cave near Ava when he collected there in August, 1932. F.M.N.H.—18603, 23712, 23713, 18605; S.I.N.U.—138, 194, 233.

14. *Siren intermedia* LeConte. — *Siren* are common in the ponds and swamps. They are particularly numerous in the shallow, vegetation-clogged sloughs and ponds, many of which go dry during late summer and remain so through most of the winter. The *Siren* enter crayfish burrows to a depth of

several feet and remain until the area is again flooded. Considerable data has been collected on this habit and is being described in a separate publication.

Cagle and Smith (1939) described a large aggregation of this species observed near Herrin, Illinois.

Three larvae 2.8 cm. in length were collected from sloughs near the State Forest, May 17, 1939.

Garman (1892) states, "A small example of this species from Running Lake, Union county, was marked when alive with a bright orange band across the end of the muzzle and another one extending from the sides of the mouth to the bases of the branchial tufts. This remarkable batrachian is not uncommon in the mud of lakes in the southern portion of Illinois." C.M.—19078-81; S.I.N.U.—186, 273, 50, 120, 198, 269, 272, 287.

15. *Bufo americanus americanus* (Holbrook).—Rare. This species has been collected only in the Rattlesnake Canyon near Murphysboro where several pairs were observed breeding in a shallow pool, May 20, 1937. Only two *Bufo fowleri* were in the pools at that time but many were observed in the canyon area. A.M.N.H.—32726, 5582-90; F.M.N.H.—18604; S.I.N.U.—98, 162, 69, 73, 81, 105.

16. *Bufo fowleri* (Hinckley).—The most abundant amphibian. Two were collected May 20, 1937, in a pool near Murphysboro among a large number of breeding *Bufo americanus*. In the laboratory the male *americanus* clasped with the *fowleri* and a considerable number of eggs were deposited.

This species breeds from the first of April to August. Any time during this period they may be heard about almost every body of water in the area. They are not selective as to a breeding habitat and may be found in the cypress swamps, in muddy stock ponds or along the clear, rock-bottomed streams in the Mississippi bluffs region.

A female from a clasping pair collected April 28, 1939, deposited 6,050 eggs during the night.

Many young toads metamorphose during June, July, August and September. Many small specimens 1 cm. long observed during the first days of June were being eaten in numbers by small water snakes.

Bufo fowleri evidently burrows deep in the ground to escape unsatisfactory weather conditions. Mr. Moreau S Maxwell, directing an archaeological excavation crew, discovered several toads buried 6-20 inches in hard baked clay during October. These were excavated from the top of a hill overlooking a small creek. One of the toads had evidently been buried for a considerable length of time as it was much emaciated. A careful section of the earth at the site where the toads were found revealed the presence of a long burrow filled with loosely packed earth at the bottom of which was a round cavity with walls worn smooth by the movements of the toad (Figs. 5, 6). All the toads were quite inactive when found but became more active when placed in the sun. As

they were warmed they attempted to dig in with scooping movements of the rear legs.

A few stomachs were examined from specimens collected during summer months. The following materials were found in the number of stomachs indicated:

Caterpillars	1	Spiders	1	Wood chips	1
Click beetles	1	Ants	4	Cicada	1
June beetles	12	Chrysalid	1	Centipedes	4
Tiger beetles	4	Grass	1		

F.M.N.H.—18581, 18582, 18606, 18607, 23715(10), 23731(12), tadpoles, 23730(8), 23741, 23742; C.A.S.—2007, 2008; S.I.N.U.—23, 86, 277, 127, 132, 283, 161, 25, 128, 129, 180, 240, 87, 88, 92, 94, 95, 96, 97 99 100 113, 185, 221-224, 240.

17. *Acris crepitans* Baird.—Abundant. This species is first heard calling in February and their courtship continues through July.

Eggs were found in pools near Thompson Lake, Carbondale, March 21, 1937. Although water in these pools was frozen after that date the larvae apparently survived as large tadpoles were collected there in early April. F.M.N.H.—23702, 23703, 23704, 23705, 23706, 23707; C.A.S.—174-180, 181-200, 201, 2013, 2019; S.I.N.U.—65, 134, 144, 158, 250, 165, 290, 126.

18. *Pseudacris nigrita feriarum* (Baird). — Abundant. They breed from March to the last of May.

Many tadpoles collected from pools near Thompson Lake, May 10, 1939, were retained in the laboratory where they began to emerge from the water May 12. A very short tail stub was still present. Many specimens were observed emerging in the field on this same date. These varied in total length between 2.0 to 2.5 cm.

Tadpoles grown in the laboratory developed first definite indications of dorsal striations just previous to the time of appearance of the forelegs. All markings were well developed and distinct at time of emergence from the water. F.M.N.H.—18630, 18631; S.I.N.U.—220, 227, 260, 5, 43, 218.

19. *Hyla avivoca* Viosca.—A single specimen collected in Grand Canyon, Murphysboro, March, 1937, was identified by K. P. Schmidt as this species. Subsequent trips to that region have failed to yield additional specimens. F.M.N.H.—25940.

20. *Hyla cinerea cinerea* (Schneider). — Common about most swampy areas in both counties.

Tadpoles of this species were collected from a pool near Ware, May 28, 1939. This pool was about 20 feet long and 10 feet wide and was bordered with a heavy growth of weeds and willows. Larvae of *Rana pipiens, Bufo fowleri,* and *Hyla versicolor* were collected at the same time.

When the tadpoles were taken to the laboratory one specimen had four legs and the others only the two hind legs. By May 30, one frog had emerged from the water. It had a tail stub 1.4 cm. long and green coloring was apparent only on the back of the head. By June 2, the entire back had changed to a light green and by June 3, leg bands were obvious and the legs and arms were green. A tail stub was still apparent.

21. *Hyla crucifer* Wied.—Common in low, wet areas. They were frequently collected as they clung to the rock walls above the clear shallow pools at the base of the bluffs along the Big Muddy River. They could always be collected in abundance during the breeding season which extends from the first week of March to June.

Ten males and three females were collected March 18, 1940, from calling positions at the edge of the water or on vegetation growing in a slough near Carbondale. The air temperature was 12°; water temperature 10°. None of the three females collected had deposited their eggs.

Males were sometimes heard calling during the day but no clasping pairs were ever found during daylight hours.

Tadpoles were very numerous in pools adjacent to the railroad track near Ware, May 27, 1939. These pools were checked carefully June 8, 1939, and all larvae had metamorphosed. F.M.N.H.—11747, 18583, 23696, 23697, 23698, 23699, 23700, 23701, 25936-1; C.A.S.—2015; S.I.N.U.—193, 195, 219, 259, 270, 115.

22. *Hyla versicolor versicolor* (Le Conte).—This species is common in the area and is easily collected during the breeding season. Breeding aggregations may be found between the first of April and the last of July but the peak of the season usually occurs about the middle of May.

Twenty-four specimens were collected from willows growing in a shallow pond at the base of a steep bluff near Murphysboro, June 14, 1938. A few *Hyla cinera* were collected at the same time but none were observed clasping. The *Hyla versicolor* were clasping and depositing eggs.

Thirteen breeding specimens were collected in a small, gravel bottomed stream about four feet wide and two feet deep south of Alto Pass, May 18, 1939. The water temperature was 20° C. and air temperature 21.5° C. The males were calling vigorously and continued to do so after they had been placed in collecting sacks. Two were calling from a cluster of elms growing on a bank of the stream; others were calling from the ground. One clasping pair was almost completely submerged with only the heads anterior to the eyes visible. The female deposited eggs in the laboratory.

The area within a 25 foot radius of this breeding aggregation was checked carefully for other amphibians and specimens of *Rana catesbiana, Rana clamitans, Rana pipiens, Acris gryllus,* and *Bufo fowleri* were collected Only the *Bufo fowleri, Rana pipiens,* and *Acris gryllus* were heard calling.

Tadpoles with fore and hindlegs developed were collected one-half mile

south of Ware, May 30, 1939. C.A.S.—2009; F.M.N.H.—18585; S.I.N.U.—11, 20, 151, 154, 225, 7, 10, 44, 238.

23. *Rana areolata circulosa* Davis and Rice.—Mr. Philip Smith, who has studied the gopher frog during the past two years, has kindly provided the following notes:

The gopher frog is abundant in southern Illinois. At the height of their breeding season as many as 500 individuals were estimated in a small pool 40 x 100 yards. In this pool 179 egg masses were removed from an area of about ten square feet.

Small temporary pools in fields and along roadsides usually contain many breeding pairs.

On two consecutive nights of collecting 289 individuals were collected from several small ponds.

The breeding dates are incompletely known. In 1938 many were collected on March 19. Mr. Jack Henderson said that approximately two weeks earlier he collected over one hundred in one evening. In 1939 the first specimen was observed on March 3 but no calling was heard until March 5 when the frogs were calling from their holes in the fields. The first pair of clasping frogs was found on March 9.

On March 14, 1939, several small ponds were examined for egg masses and a count made. Three small temporary ponds contained, respectively, 115, 125, and 75 egg masses. These ponds were within 100 yards of each other.

By March 15 there was a definite decline in the number of frogs in the pools. On March 22 they were again heard calling from the holes in the fields but some were still in the ponds. By April 14 all of the frogs had left the pools.

In 1940 a single, clasping pair was taken from Thompson's Lake, Carbondale, on April 23.

Larvae emerged from the masses laid during early April in the pools near Herrin on March 24.

Wright and Wright (1933) states that the gopher frog metamorphose during the first week in July at a size of 30 mm. On June 25, 1938, no tadpoles or young frogs could be found in and around the ponds which contained many tadpoles a few weeks earlier. On July 8, 1939, about 25 metamorphosing *areolata* were collected from a drying pool. The body length of preserved specimens (body length considered length from end of snout to insertion of hind legs) averaged 22 mm. S.I.N.U.—1, 160, 29, 4, 208, 192, 209, 274, 55, 68, 47.

24. *Rana catesbeiana* Shaw.—Abundant about the margins of lakes and swamps and particularly so in the cypress swamps of southwestern Union county.

Numerous individuals were observed breeding in Thompson's Lake near Carbondale, June 12, 1938. They may be collected along the margins of lakes and ponds any time during the spring or summer.

The tadpoles usually overwinter and transform during the last of April or the first of May. Occasional specimens complete the metamorphosis in one season.

Twenty-five stomachs taken from frogs collected May 26, 1939, contained the items in the following list. The numbers indicate in how many stomachs each item was found:

Turtles	2	Snails	7
Crawfish	9	Ants	1
Aquatic insect larvae	4	Cricket	1
Aquatic beetles	5	Elm seeds	2
Terrestrial beetles	5	Willow leaves	3

The turtles were hatchling *Chrysemys picta* ssp. Crawfish constituted the dominant food. A.M.N.H.—32313, 32310, 32252, 23358; S.I.N.U.—8, 262, 285, 74, 210-212, 214.

25. *Rana clamitans* Latreille.—The green frog is abundant in and about the larger ponds and lakes. They begin to breed about the first of June and some pairs may be observed in late July. F.M.N.H.—23725(2), 23740; A.M.N.H. —32253, 32254-57; S.I.N.U.—173, 213, 232, 256. C.M.—4623.

26. *Rana palustris* Le Conte.—Rare. Garman (1892) records a specimen from Bluff Lake in Union county and notes that this species is rare throughout Illinois. C.A.S.—214, 215; S.I.N.U.—239.

27. *Rana pipiens* Schreber.—This species may be collected in abundance from the streams and ponds by the first of March. They breed in March and April.

The tadpoles transform during June and July. Many were observed at the city reservoir June 7, 1939, as they were emerging from the water and seeking concealment in the grasses about the shore. They were 3 cm. in length with tail stubs 0.5 cm. long.

Recently transformed specimens collected May 30, 1939, near Carbondale averaged 3.6 cm. in total length with average tail stub length of 1.6 cm. A.M.N.H.—32245-51, 32278-80, 32295-97, 32299, 26652; C.A.S.—2004-2005; S.I.N.U.—2, 153, 156, 171, 176, 6, 207, 229, 261, 265, 147, 140, 255.

28. *Rana sylvatica cantabrigensis* Baird.—The wood frog is not common but may be collected during early spring from the wet ravines of the Mississippi bluffs.

There has been some question as to the systematic position of the frogs from this region. Dr. K. P. Schmidt (1938) after demonstrating a geographic variation gradient in lengths of these frogs, states, "It is by no means clear that the wood frogs of southern Illinois are properly referable to *Rana sylvatica cantabrigensis*, but it is preferable to associate them with the western subspecies unless other characters than leg length can be found to differentiate them."

Measurements of available specimens from the region fall within those

given by Schmidt (1938) in his discussion of a geographical gradient. The t/b of six specimens from Murphysboro was .62, .61, .60, .59, .57. S.I.N.U.—133, 172; F.M.N.H.—25938, 25939.

29. *Sceloporus undulatus undulatus* (Latreille).—On warm, sunny days this lizard may be observed in numbers in any dry, open woodland where there is fallen timber or rock exposure.

A copulating pair observed on a large rock in a canyon west of Murphysboro, May 3, 1938, were startled by the sudden appearance of the collector and remained still until they were picked up. The male continued to cling to the female after they were dropped into the collecting sack. A dissection of the female indicated the presence of 13 ovarian eggs averaging 6 mm. in diameter. There were no eggs in the oviducts.

Several pairs were observed in copulation near the overflow of Midland Hill's Lake, May 7, 1939. All were very active. The air temperature was 31.5° C.

A specimen laid eight eggs in a laboratory terrarium August 1, 1940. They were buried one-half inch deep in loose dirt and measured 1.35 cm. x 0.72 cm., 1.34 x 0.78, 1.36 x 0.75, 1.37 x 0.72, 1.30 x 0.72, 1.33 x 0.72, 1.33 x 0.79, 1.37 x 0.74. An attempt was made to incubate the eggs in moist wood rot, but they all shriveled within a few days. F.M.N.H.—11761, 11762, 13214, 13215, 18614, 18615, 23728, 23729; S.I.N.U.—7, 24, 39, 503, 579, 460, 461, 502.

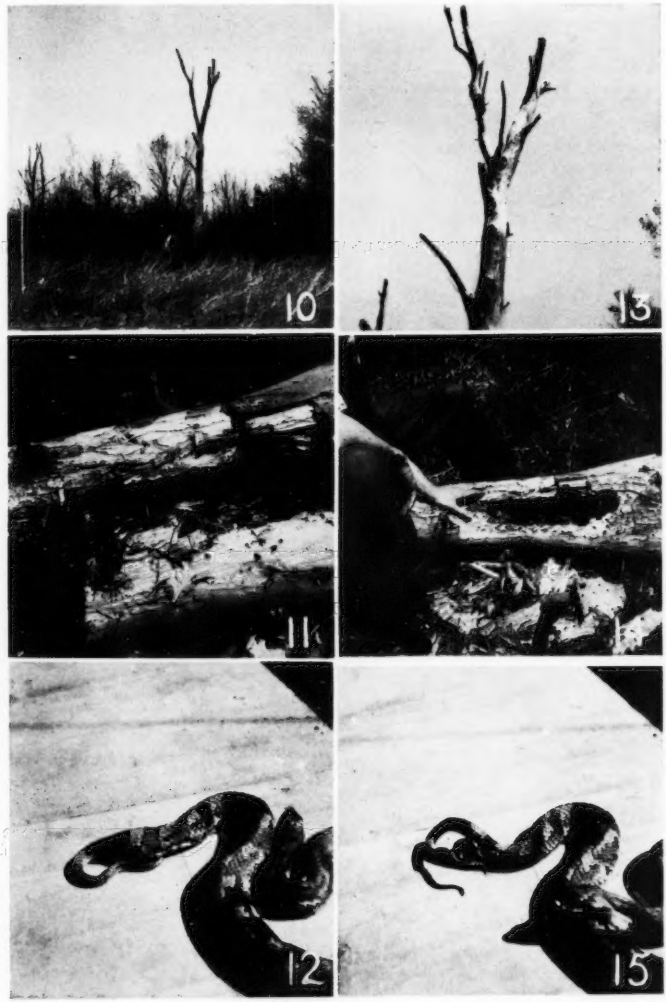
30. *Cnemidophorus sexlineatus* (Linné).—No specimens have been collected but the species probably occurs here. Garman (1892) states that they were not rare at Henry on the Illinois River and that he thought he saw a specimen at Cave-in-Rock.

31. *Leiolopisma unicolor* (Harlan).—This small, active lizard is the least abundant of the lizards. Specimens were taken along the dry margins of cypress swamps in Union county, in the low oak-hickory forests of northeastern Jackson county, and the beech-maple forests at the foot of the Mississippi bluffs. S.I.N.U.—539, 623, 624, 5; C.A.S.—57.

32. *Eumeces fasciatus* (Linné).—Abundant in the drier portions of oak-hickory woods. The eggs of this lizard may be collected abundantly from the interior of fallen logs during June and July. The eggs are brooded by the female and hatch during the last of August or the first of September. Observations on the breeding habits of this species in this area were described by Cagle (1940). F.M.N.H.—11740, 11741, 11742, 11743, 11759, 11760, 23726, 23727; C.A.S.—25-26, 2003; S.I.N.U.—12, 18, 551, 83, 520, 542, 28, 537, 11, 80, 280.

33. *Carphophis amoena helenae* (Kennicott).—The worm snake was collected on four occasions from areas where there were fallen, decaying timbers. All specimens were found under or within these fallen logs.

34. *Farancia abacura reinwardtii* (Schlegel).—This species apparently occurs



Figs. 10, 13.—A dead tree serving as a temporary home of a chicken snake. Note the height of the tree as compared with the man at its base. Fig. 13 shows clearly the entrance to the cavity. Fig. 11, 14.—The cavity opened with an ax to show its extent and the snake coiled within. Fig. 12, 15.—A spreading adder depositing an egg. These pictures were taken two minutes apart.

in two isolated populations. Five specimens have been reported from Perry county; eleven specimens have been collected in the vicinity of Mitchell's Lake at Herrin. Both of these regions are low and swampy with considerable fallen and decaying timber in some parts.

Mr. Philip Smith collected a large female near Herrin, June 12, 1939, from under a partially submerged log. He reported that a cavity had been hollowed out under the log as if the snake had been using it repeatedly as a retreat. This snake was preparing for ecdysis when collected.

This specimen was retained in captivity and was found coiled around a cluster of 22 eggs July 7, 1939. The eggs were deposited on top of damp wood rot; apparently the ♀ had made no effort to bury them in this material. The eggs were white with thin flexible shells and were very irregular in shape. The maximum size was 3.83 by 2.07 cm.; the minimum 2.90 by 1.67 cm.; average length 3.45 cm.; average width 1.99 cm.

This female, like the one described by Meade (1937), apparently attempted to retain the cluster of eggs in the coils formed by her body. When disturbed, she merely tightened the coils slightly or jerked her head about.

All the eggs were removed to a glass bowl and incubated in moist wood rot at room temperature. Several eggs were opened by Dr. Hugh Clark during progress of incubation; the remaining ones hatched August 13. Three of the young measured respectively 22.5, 25.6, 24.0 cm. They were quite active and burrowed deep into the moist wood rot immediately after leaving the egg.

The incubation period was 41 days, one week shorter than reported for two clutches of *Farancia* eggs in Louisiana that were kept under similar conditions.

This female fed actively on *Siren* which are abundant in the area from which it was collected. It ate six large *Siren* in three days. S.I.N.U.—399, 341, 608, 591.

35. *Diadophis punctatus arnyi* (Kennicott).—A specimen collected near Grand Tower and another at Chester have been assigned to this subspecies. S.I.N.U.—73, 536.

36. *Diadophis punctatus strictogenys* Cope.—This species has been reported as occurring in abundance near Alto Pass where one collector reported that 75 had been collected in the last two years. One specimen was collected from under a large log in a pasture near Murphysboro in 1938 and several other specimens have been reported from high school collections. S.I.N.U.—535, 270, 192, 89.

37. *Heterodon contortrix* (Linné).—The spreading adder is abundant in the plains region of the area but is rarely taken in the bluffs along the Mississippi flood plain. Commonly regarded as poisonous it is usually not molested, although frequently found within the boundaries of villages and towns.

A large female laid 35 eggs in the laboratory June 7, 1939 (Fig. 12, 15). Twenty-four of the eggs were opened during incubation and the remaining eleven hatched July 7. Four of the eleven were the red phase and the remain-

ing seven the normal dark color. They measured in total length 20.5, 20.7, 21.2, 20.0, 19.4, 20.7, 20.1, 20.7, 21.1, 31.5, 20.9 cm. respectively.

Another female deposited four eggs June 26, 1939. Two of the eggs were opened before hatching and the remaining two hatched August 14; an incubation period of 50 days.

During late September, 1937, Roy Reeves, Murphysboro, found a group of *Heterodon* eggs under a rock. The eggs hatched in a few days after they were collected.

Numerous young specimens have been collected on the S.I.N.U. campus during September for the past three years. Three specimens collected September 10, 1938, had apparently just hatched as the umbilicus was still open and the egg tooth scar apparent. They measured 22.5, 23.5, 22.4 cm. in length. C.A.S.—1596, 2516; S.I.N.U.—61, 67, 109, 149, 494, 495, 529, 574, 612, 585, 570, 427, 425, 424.

38. *Opheodrys aestivus* (Linnaeus).—The rough green snake is abundant about the margins of woodlands throughout the region. U.S.N.M.—56387-89 59036; C.A.S.—1583, 2539; S.I.N.U.—59, 62, 66.

39. *Coluber constrictor constrictor* (Linné).—The blacksnake, one of the most abundant snakes of the region, is most frequently collected in thin woods along streams where they sometimes climb to a height of fifteen feet or more on trees and vines. One was collected near Ava at a height of fourteen feet up in a tree overhanging a creek bank.

Most of the specimens from this area are intergrades between the two subspecies, *Coluber constrictor constrictor* and *Coluber constrictor flaviventris*.

The eggs are laid during the last of May through June and July. A group of eggs was plowed up by a farmer in July, 1935, who reported that they were apparently buried in a crayfish hole.

A female laid 21 eggs in a laboratory cage, June 26, 1940. The average length of the eggs was 3.0- cm.; maximum length 3.35 cm.; minimum 2.78 cm. Another female laid 20 eggs July 10, 1940. This group of eggs was unusual in that every egg was flattened on each end as if it had been forced against the adjacent egg in the oviduct. One egg was hardened and shriveled.

The eggs were measured and weighed soon after they were deposited.

Length	Width	Weight	Length	Width	Weight
2.15 cm.	1.57 cm.	3.90 gr.	2.69 cm.	1.69 cm.	3.95 gr.
2.08	1.60	3.55	2.05	1.53	3.06
2.20	1.60	3.83	2.64	1.58	3.90
2.37	1.65	4.50	2.52	1.52	3.90
2.07	1.60	3.80	2.49	1.48	3.60
2.12	1.62	3.80	2.40	1.71	4.50
2.15	1.61	3.60	2.50	1.61	3.70
2.23	1.60	3.90	2.48	1.55	3.75
2.55	1.56	4.3	2.55	1.46	3.80
2.30	1.55	3.75			

Both groups of eggs were incubated in moist wood rot at an average temperature of 20° C. Eggs from the second brood hatched September 6, 7, 1940. The young snakes fed readily on pieces of earthworms.

The adults have a wide variety of foods as indicated by the following records. The number indicates the number of stomachs in which the particular item was found:

Grasshoppers	1		
Peromyscus	2	Natrix	1
Microtis	2	Opheodrys	1

A specimen collected from a rocky stream bed at 2:30 p.m., May 7, 1939, contained a striped chipmunk *(Tamias striatus)*. A male three feet long collected in Indian Creek Valley, October 25, 1939, contained two rough green snakes. The largest specimen was 45 cm. long and the other a newly hatched specimen. The larger specimen had been folded several times as it was swallowed. The two green snakes were the first records of the species from this particular region. U.S.N.M.—94362; S.I.N.U.—68, 86, 102, 138, 140, 411, 141, 285, 595, 584, 445; F.M.N.H.—18650, 18653, 18651, 18654, 19274, 23735.

40. *Elaphe obsoleta obsoleta* (Say).—The pilot black snake is abundant over the entire region but has been collected in most abundance from the forested canyons of the bluff area. They were often found in very wet areas.

On two different occasions this species has exhibited an interesting protective instinct. A specimen observed on top of a large stump literally froze in position with the posterior part of its body coiled around a projection of the stump and the anterior end protruding outward for a distance of one foot. In this position it resembled the broken branch of a tree and its color contributed much to this impression.

A large male was observed on a decaying cypress stump near Belknap, Illinois. It also remained very quiet until touched by the collectors. Even then it exhibited an unusual disposition in that it refused to leave the stump and go into the water surrounding it. Although picked up and examined for stomach contents, it displayed no fear of the collectors.

These snakes are excellent climbers and were collected from trees on several occasions. While observing birds near the Carbondale city reservoir, April 30, 1939, Lendell Cockrum noticed what appeared to be a snake's head protruding from a woodpecker's hole about 35 feet up a dead tree approximately 20 inches in diameter at the base and completely devoid of bark (Figs. 10, 11).

The tree was cut down and the opening enlarged. A large female *Elaphe* was coiled within a cavity 16 inches long and nine inches in diameter (Fig. 11, 14). The snake was obviously the third inhabitant as the cavity had been excavated by a woodpecker and a family of flying squirrels had lined it with a thick layer of grasses. The body of a flying squirrel that had been swallowed and regurgitated by the snake was found in the cavity. As the cavity had only one entrance, it was necessary for the snake to climb the smooth tree to enter. The

snake was taken to the laboratory where its length was determined at 52½ inches and total weight 588 grams.

A specimen found dead near Etherton, September 11, 1938, had swallowed a large chipmunk *(Tamais striatus)*. The chipmunk had obviously been dead for some time before the snake had swallowed it. C.A.S.—2030, 2519, 1590, 2035; F.M.N.H.—18655, 18656, 19262; U.S.N.M.—56595-96; S.I.N.U.—137, 139, 143, 491, 613, 587, 599.

41. *Lampropeltis calligaster* (Harlan).—This, the most abundant king snake of the region, is frequently collected in open fields adjacent to creeks and ponds. It has been collected on numerous occasions from wheat fields during harvest.

A W.P.A. crew found nine eggs August 17, 1940, buried six inches under the surface in loose soil. Five of the eggs examined in the laboratory measured in length 4.9, 4.5, 4.4, 4.4, 4.9 cm.; width 2.5, 2.5, 2.8, 2.7, 2.4 cm. One of the eggs contained a well developed snake 27 cm. in total length. The other four eggs were incubated in moist wood rot but did not hatch. S.I.N.U.—493, 497, 554, 594.

42. *Lampropeltis triangulum syspila* (Cope). — The red snake is not common and has been collected at infrequent intervals; only 10 specimens were reported during four years. Five of these were collected by C.C.C. camps in Union county. S.I.N.U.—79, 90, 93, 136, 161.

43. *Lampropeltis getulus holbrooki* (Stejneger).—The speckled king snake is common throughout the area and is most frequently collected in uncultivated open fields and thin woods.

A female deposited nine eggs in a laboratory cage during the night of June 18 or early morning of June 19, 1939. Dr. Hugh Clark retained these eggs to secure embryological material and kindly provided the following data.

Measurements in mm. of length and greatest diameter of each egg were: 41-20; 40-21; 41-20; 38-20; 41-18; 42-19; 45-18; 45-20. None of the eggs died but some were opened before hatching. One of the remaining three eggs hatched at 10:45 a.m., August 12, and two others were ready to hatch but the snakes did not emerge until the morning of August 13. These eggs were retained in moist wood rot and the container kept in a room where the average temperature was about 75° F. The incubation period was thus 54-55 days. This interval is much shorter than that recorded by Blanchard (1932) who studied a group of *holbrooki* eggs that required 77-78 days for incubation.

One of the specimens escaped; the other two measured 30 cm. and 29 cm. respectively in total length three days after they were hatched. The larger of these was placed in a jar with a number of *Farancia abacura* that had just hatched. It immediately attacked several in succession and finally swallowed one that measured 22.5 cm. in total length.

It is apparent that eggs may be deposited earlier and hatch earlier than the clutch described as on two different occasions just-hatched snakes have been collected during early July. Three young each approximately 23 cm. in length

were collected near the Campus July 6, 1936. These were not over a few days old as the umbilical opening was still unhealed.

Another recently hatched specimen was collected near Makanda, Illinois, July 10, 1939.

Specimens fed readily in the laboratory on mice and snakes. One swallowed a *Natrix sipedon* about one-third its own length after suffocating it by constriction but regurgitated it the next day. Another snake refused to eat water snakes but readily accepted other kinds. Blanchard (1921) stated that Mr. Mackelden of St. Louis observed that the king snake seemed to have an aversion to garter snakes and water snakes as food.

Another captive specimen swallowed a small copperhead within two minutes after securing a grasp on its neck. A large female collected near Elkville contained an adult meadow vole. C.A.S.—70, 1580; F.M.N.H.—23743; S.I.N.U.—57, 95, 104, 135, 142, 556, 588.

44. *Natrix cyclopion cyclopion* (Dumeril and Bibron).—Although several hundred *Natrix* from this area were studied, no *Natrix cyclopion* were found.

Garman (1892) describes a single specimen from Bluff Lake, Union county.

45. *Natrix erythrogaster erythrogaster* (Forster).—The red-bellied water snake is most abundant in the sloughs and muddy drainage ditches of the Mississippi flood plain. It was rarely collected in the clear rock bottomed streams where *Natrix sipedon* abounds. This is one of the first snakes to appear in the spring. One was observed basking on the shore of Corbin Lake, March 10, 1939.

A pair were observed in copulation near Murphysboro, May, 1934. They were coiled together on a rock ledge above a small stream and were moving in a slow, rhythmic fashion. The male escaped into the water when startled but the female was collected. Dissection indicated the presence of 28 large ovarian eggs.

A specimen collected from Crab Orchard Creek contained one large *Lepomis humilis* and the chela of a large crawfish. S.I.N.U.—75, 220, 252, 467, 468.

46. *Natrix grahamii* (Baird and Girard).—Mr. R. M. Perkins states in correspondence that he collected *Natrix grahamii* at the snake dens near Murphysboro.

Specimens in the S.I.N.U. Museum was collected at Duquoin, May, 1927, and Elkville, in 1940.

Mr. Philip Smith collected one from a mine pond near West Frankfort but the specimen was subsequently lost. S.I.N.U.—144, 118.

47. *Natrix rhombifera rhombifera* (Hallowell).—This species is common along the margins of the larger streams and lakes.

A large female collected from Grimsby Lake, June 1939, was in the process of ecdysis. Collectors observed 15-20 sloughs in approximately one

acre of the shallow water and another *Natrix* was observed in ecdysis. The sloughs were floating or wrapped about the aquatic plants that crowded the shallow water. Such an accumulation of shed skins was most unusual. Klauber (1938) observed 10-12 recently shed skins of *Thamnophis ordinoides elegans* about a boulder in El Dorado, California. Such observations tend to suggest uniformity of ecdysis in a given population.

A captive specimen ate 17 small *Rana*. Another specimen collected near Herrin contained a catfish 6 inches long. C.A.S.—87; S.I.N.U.—492.

48. *Natrix sipedon* ssp. (Linné).—The most abundant snake of the area. Any body of water may yield a surprisingly large collection of this species to skilled collectors.

The majority of the specimens studied were intergrades between *Natrix sipedon sipedon* and *Natrix sipedon pluralis*. Both subspecies and a wide range of intergrades may be collected from the same stream. As the subspecies were not separated during field observation the following notes relate to *Natrix sipedon* ssp.

They are most abundant in the clear streams of southern Jackson and Union counties. On one trip to a shallow gravel bottomed section of Hutchins Creek, May 18, 1939, five small *Natrix sipedon* were collected within an area of 4 square feet where the current was strong. One of these was resting under a flat rock with only its head visible. Another had a section of its body looped around a rock in order to hold its position in the swift current.

Numerous minnows were spawning in these ripples and were probably the attraction for the snakes, although none were found in the stomachs of seven specimens collected.

On May 31, 1939 at 6 a.m. 7 snakes were collected at a small muddy pond near Carbondale. Five of these were in the water but were concealed under rocks and logs; two were under rocks on dry land. Five contained small sunfish *(Lepomis humilis)*. After removal of the stomach contents, the snakes were released. On five successive early morning trips to this pond over a period of three weeks three to five *Natrix* were collected at each visit. In every case but three they had been feeding on small leopard frogs or sunfish.

Two large specimens were collected in Thompson Lake May 8, 1939. One contained a large bullfrog and the other had not been feeding. Many such similar observations as the above indicate that the great majority of these snakes feed at night and remain concealed or bask during the day.

Two specimens were observed in copulation on the bank of a farm pond near Etherton, April 29, 1939. They were coiled together on a sunny bank two feet above the water and were moving slightly when first observed. When startled, they separated and fled to the water but both specimens were collected.

A brood of 16 was born Sept. 8. Two of these died because they were unable to penetrate the embryonic membranes.

A large female collected near Carbondale, August 6, 1937, was swimming slowly very close to shore and was easily captured because of the weight of

the embryos she carried. On August 17 she gave birth to 44 young. The smallest was 18 cm. long; the largest 26 cm.

Several other broods have been born during August and Sept. in the laboratory. C.A.S. — 2520-30; U.S.N.M. — 56645-49; F.M.N.H. — 23732, 11748; S.I.N.U.—65, 81, 106, 223, 395, 396, 401-5, 407-8, 446, 464-71, 504-8, 573, 308, 609-10, 103, 112, 576-77, 559-566.

49. *Storeria dekayi* (Holbrook).—Specimens have been collected only in oak-hickory lowland forests near Anna where they are abundant.

A gravid female was found July 22, 1939 under the loose bark on the upper side of a fallen tree in such an area. On August 7, she gave birth to 8 young. These measured in length 8.2, 8.7, 9.6, 10.1, 9.9, 9.9, 9.0, 10.1 cm. respectively.

Mr. Norman Meinkoth and Mr. Philip Smith have reported several specimens from the vicinity of Herrin. F.M.N.H.—18617; S.I.N.U.—251, 273, 568, 119, 589.

50. *Storeria occipitomaculata* (Storer).—Garman (1892) records a specimen from Anna. A single specimen collected in Carbondale 1884, is deposited in the S.I.N.U. Museum, and another from Murphysboro is in the Field Museum. F.M.N.H.—23716; S.I.N.U.—392.

51. *Haldea striatula* (Linné).—Mr. R. M. Perkins states in correspondence that he collected one specimen at the snake dens near Murphysboro just after a hard rain. No specimens from this region are now available in museum collections.

52. *Haldea valeriae elegans* (Kennicott).—The only specimen collected during the survey was taken by Lendell Cockrum from under a large log in a thick oak-hickory forest north east of Elkville, Oct. 11, 1940. The specimen is a male measuring 21.4 cm. in total length; tail length 4.5 cm. Scale rows 17-17-17; ventrals 125. This secretive species is undoubtedly more abundant than indicated by this single record.

Kennicott (1859) states that these snakes are found in the "heavily timbered regions of southern Illinois." Garman (1892) listed a specimen of *valeriae* from Union county but Blanchard (1923) says, "H. Garman's record (1892, p. 308) of *valeriae* for Union county, Illinois, was more likely based on a specimen of elegans."

R. M. Perkins reported in correspondence that he had collected this snake near Murphysboro. S.I.N.U.—620; C.A.S.—126.

53. *Thamnophis sauritus sauritus* (Linné).—On August 8, 1936 and August 30, 1937 recently born specimens were collected from forest debris in the mouth of a cave at the foot of Chalk Bluff near Murphysboro. In both instances it was apparent that the young snakes had been born only a few hours. S.I.N.U.—621-2.

54. *Thamnophis sirtalis sirtalis* (Linné).—Abundant throughout the area.

A female 85 cm. long gave birth to 53 young, July 7, 1939. The largest young was 19.2 cm. in length; the smallest 16.2 cm. C.A.S.—2526, 2317-18; U.S.N.M.—56075, 56076, 99157; S.I.N.U.—69, 84, 113, 398, 410, 72, 496, 541, 586, 546-7.

55. *Agkistrodon mokasen cupreus* (Beauvois).—The copperhead is common in the dissected hills area bordering the flood plain. They were frequently collected during early spring and late fall from the dens at the foot of bluffs along the Mississippi. Many of them are killed during harvest in the bottomlands of the creek valleys.

A female gave birth to eight young Sept. 10, 1939. They measured 24.2, 21.8, 24.7, 23.7, 24.0, 23.0, 23.8, 23.0 cm. respectively in total length. S.I.N.U. —267, 287, 279, 540, 578; C.A.S.—1579, 1604.

56. *Agkistrodon piscivorus* (Lacépède).—The cottonmouth is common in the valleys of the larger creeks and rivers and is particularly abundant along the lower reaches of the Big Muddy River.

They may be collected in large numbers during early spring or late fall from the dens at the foot of the bluffs. Hundreds are killed each year by snake hunters who regularly visit the dens for snake shoots.

The females often return to the dens during the last of August or the first of September to bear their young. A specimen collected from a den in Union county, September 3, 1936 gave birth to five young September 4. Several young snakes were collected in September, 1938, at the entrance to a shallow cave in Rattlesnake Canyon. U.S.N.M.—824, 826, 12643; F.M.N.H.—18659; C.A.S.—1605; S.I.N.U.—372; U.M.Z.—68432.

57. *Crotalus horridus horridus* Linnaeus.—Both *C. h. horridus* and *C. h. atricaudatus* are common in some portions of the dissected uplands. They may be collected in abundance about dens along the Mississippi bluffs during early spring or late fall. One collection may yield specimens of *horridus*, *atricaudatus*, and specimens intermediate between them. S.I.N.U.—274-5, 409, 489, 88, 99, 123; F.M.N.H.—18657, 18658, 23736.

58. *Crotalus horridus atricaudatus* Latreille.—Common in the dissected uplands and along the Mississippi bluffs. M.Z.U.M.—68477, 79400.

59. *Sternotherus odoratus* (Latreille).—The musk turtle is common in all the waters of the area, but is most abundant in the shallow, mud bottomed, vegetation choked lakes. Numerous specimens were frequently observed in the edge of the water during night collecting throughout the spring and summer and a few sweeps of the hands over almost any muddy bottom in shallow water would yield several turtles.

When the water cools to a few degrees below 10° C., the turtles burrow into the bottom under a few inches of water until they are buried under one or two inches of mud. They then force their head upward and stretch the neck until they can push the tip of their nose above the water for air. The hole left by the retreating head is the only evidence of the turtles presence

unless one is fortunate enough to observe the turtle in the action of securing air. This habit has been repeatedly observed and turtles collected from such mud retreats. *Chelydra* uses the same method for semi-hibernation. One *Sternotherus* was observed in such a position Dec. 1, 1939 and the position noted. On two later dates, Dec. 6 and Dec. 9 the turtle was in the same place. It was collected on Dec. 9 and examined in the laboratory.

The alimentary tract was empty. It appears that turtles of this species may not eat during the winter months when the water becomes cold. Thus of 14 specimens examined during November, December, January and February none contained any material in the digestive tract. Stomachs and intestines of six specimens collected at the City Reservoir March 22, 1940 were empty.

Seven specimens collected from Elkville City Lake, April 27, 1940 were buried in dense masses of aquatic vegetation from which they were collected by muddling. The stomachs and intestinal tracts of all were packed with fragments of small clams. Although many crayfish were present in the lake there was no evidence that the turtles were using them for food.

Three specimens collected from a one acre clear pond near the City Reservoir, June 22, 1940 had been feeding on a dead chicken in the water. All stomachs contained feathers and flesh; one turtle had swallowed 10 feathers, each measuring 10 cm. in length. They filled the entire stomach and projected into the small intestine. The large intestines of the three turtles contained fragments of crayfish.

A turtle collected from the shallows of the City Reservoir, June 15, 1940 had remains of one beetle in the stomach and the wing covers of 3 others (Coccinellidae) in the intestine. The entire intestine was packed with remains of crayfish.

The turtles begin to lay their eggs in late May and some may be observed laying as late as July. The chart gives egg laying data on a few of the turtles collected during the last two years.

A specimen observed at Horseshoe Lake, June 10, 1939 was attempting to burrow under a log about 60 feet from the water and was so intent on its task that it ignored the observer. It burrowed by forcing its head under the log and then pushing mightily with the rear legs. After a few minutes it found the task impossible and turned to crawl under a pile of dried leaves, remained motionless for a few minutes, then looked about and crawled toward another log. It was collected and when examined contained four eggs ready to be laid.

Another individual observed on the same date was crawling under a pile of lumber. Most of the nests found were under logs or other objects. Nests were often so shallow that the eggs protruded from the soil.

Five eggs dissected from a female collected June 6, 1940 were incubated in moist wood rot at an approximate average temperature of 20° C. The eggs hatched Sept. 16, 1940; an incubation period of 102 days. Risley (1933) states, "The incubation period of the eggs of this species is also somewhat

Egg Data—*Sternotherus odoratus*

			No. of Eggs		Egg Measurements					
Date	C.L.	Wt.	Right oviduct	Left oviduct	1	2	3	4	5	6
6-7-39	11.4	193.7	2	2	L. 3.1	3.2	2.6	2.7		
6-7-39	10.9	163.2	2	2	L. 3.0 w. 1.5	3.0 1.6	BR.	BR.		
6-7-39	9.0	115.7	1	2						
6-7-39	10.8	176.8	1	3	L. 2.6 w. 1.5	2.7 1.5	2.9 1.4	BR.		
6-10-39	10.0	....	3	2	L. 2.6 w. 1.6	2.6 1.5	2.7 1.7	2.7 1.6	BR.	
6-4-40	11.0	190.0	2	2	L. 2.9 w. 1.57	2.92 1.52	2.70 1.52	2.80 1.59		
6-4-40	10.5	170.0	3	2	L. 2.85 w. 1.60	2.80 1.60	2.72 1.60	2.80 1.61	2.80 1.61	
6-14-40	8.1	....	1	1	L. 2.62 w. 1.40	2.57 1.35				
6-15-40	9.5	....	1	1	L. 2.93 w. 1.70	2.91 1.64				
6-15-40	11.55	....	2	4	L. 2.7 w. 1.45	2.73 1.50	2.70 1.50	2.65 1.43	2.65 1.45	BR.

variable; however, embryos kept in the laboratory usually hatched in from sixty to seventy-five days after the eggs had been laid. This figure may be somewhat low, since the data were taken from embryos that had been kept in a room which occasionally reached a high temperature (37 degrees C.)." He further states, "By keeping eggs in the basement of the laboratory where the temperature rarely exceeded 25 degrees C., the incubation period was lengthened to approximately ninety days."

The hatchling turtles enter the water immediately after hatching. They may be collected abundantly from the margins of almost every lake and pond during October and November. Turtles collected in early October often have the egg tooth still present and have utilized little of the yolk stored within their bodies. The young turtles spend the winter buried in the bottom mud or concealed in the masses of floating vegetation. The abundant supply of yolk lasts them through the winter and young turtles collected in the early spring may have a substantial quantity left.

A detailed study of the life cycle of this species is now underway. A preliminary report on some phases will be published within the next three years. S.I.N.U.—475, 618, 619, 97.

60. *Kinosternon subrubrum subrubrum* (Lacépède).—This species is rare. Specimens have been collected from a sewage disposal ditch near Herrin; a drainage ditch on the flood plain and from the swamps in north eastern Jackson county.

Mr. Lendell Cockrum found 3 carapaces of this species within a few feet

of each other on a ridge adjacent to Schneider Lake, Oct. 11, 1940. S.I.N.U. —78, 382, 390.

61. *Macrochelys temminckii* (Holbrook).—This southern species has been rarely recorded from the area. Cahn (1937) mentions a specimen weighing 96 pounds that was collected at Murphysboro.

62. *Chelydra serpentina* (Linné).—Abundant. Although serious efforts have been made by sportsmen to eliminate the snapping turtles from many lakes there has been little evidence of decrease in abundance. The shallow lakes and swamps support large populations.

Most of the females deposit their eggs before mid-June. Many nests that had been excavated by mammals were studied at Horseshoe Lake, June 11, 1939. In such disturbed nests most of the egg shells were still about and a count could be readily made of the total number. The chart indicates data on some of these nests. The turtles prefer a wooded ridge several feet above water level and often dig the nest at the base of a tree.

Nest Data—Horse Shoe Lake, June 11, 1939.

Distance from water	Nest Depth	No. of eggs	
30′	17 cm.	31	Nest shaded entire day; surrounded by weeds.
20′	17 cm.	20	At side of road in weed patch at base of tree.
3′	10 cm.	20	At base of a large tree; a root 1″ in dia. ran diagonally through nest cavity.
55′	....	Ap. 30	
55′	18 cm.	8	In grass; exposed to sun most of day.
75′	17 cm.	18	At the base of a large tree; nest entrance between two large roots.

Eight excavated nests within 12 feet of the water were found on an elevated ridge along Grimsby Lake, June 7, 1940. Two undisturbed nests found within a few inches of each other were on the side of a steeply sloping bank about four feet from the water and two feet above its level. The first nest contained 20 eggs buried in a jug shaped cavity 4 inches deep; the second nest was similarly constructed and contained 31 eggs. These eggs contained no apparent embryos.

The eggs were inclubated in moist wood rot at an approximate average temperature of 20° C. Both groups hatched Sept. 5, 6, 1940 and were immediately preserved in 10% formalin. The incubation period was 90 days (assuming that the eggs had just been deposited when collected).

The turtles were measured and weighed Nov. 4, 1940. The specimens in the second group were uniformly larger than those of group one.

Measurements of Hatchling *Chelydra serpentina*

	Carapace Length			Carapace Width			Weight (grams)			Yolk Weight (grams)		
	Max.	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.
Group 1 (24)	3.13	2.4	2.86	2.93	1.87	2.65	9.5	6.0	8.28	1.4	0.5	.82
Group 2 (9)	3.7	2.85	3.16	3.0	2.67	2.90	10.7	8.3	9.39	1.1	0.5	.74
Both Groups	3.13	2.85	2.97	3.0	2.67	2.72	10.7	8.3	8.59	1.4	0.5	.79

Many of the young turtles enter the water shortly after hatching. Numerous specimens have been collected each September with the egg tooth present and the yolk mass of hatching size. Some of the turtles are often unable to escape from the nest and may remain over winter. One hatchling collected from the mud at the edge of the Big Muddy River, Nov. 18, 1937 still retained the egg tooth and large yolk sac.

The young turtles subsist on the stored yolk during the winter but specimens collected in early spring usually have rather large quantities remaining.

The chart presents data on hatchlings collected in the field.

Data on Young *Chelydra serpentina*

Date	C.L.	C.W.	P.L.	P.W.	Ht.	Wt.	Diameter of Yolk Ball
10-10-39	2.61	2.25	1.98	0.78	1.39	3.65	None present.
10-27-39	2.32	1.80	1.80	0.60		2.90	2 mm.
10-27-39	2.30	2.02	1.72	0.79	1.25	2.80	1 mm.
11-24-39	3.00	2.70				5.5	1 mm.
4- 9-39	2.30	2.02					None present.
4-26-39	2.54	1.90	1.78	0.80	1.40	2.9	1 × 2 mm.
4-27-40	2.05	1.72	1.55	0.65	1.10		5 × 6 mm.
4-28-40	2.40	1.89	1.70	0.77	1.20	3.7	1 mm.
4-28-40	2.91	2.50	1.90	1.00	1.5	4.2	None.
4-28-40	2.51	2.14	0.75	1.72	1.2	2.7	1 mm.
4-28-40	2.38	1.90	0.72	1.62	1.18	2.0	1 mm.
4-28-40	2.40	2.02	0.79	1.68	1.3	2.8	1 mm.

One specimen collected by Dr. David Thompson from a lake near Harrisburg, April 4, 1939 retained a yolk sack 2 mm. in diameter. It had been feeding as the intestines was packed with the remains of minute crustaceans.

The larger turtles move into shallow water during the colder weather and bury themselves in the mud within reaching distance of the surface. A specimen with a carapace length of 21.0 cm., weight 2200 grams, was dug from shallow mud in eight inches of water along the shore of Thompson's Lake, December 17, 1939. The intestinal tract was empty. Four other smaller specimens were located in similar situations the next day with a steel sounding rod.

Two large specimens were collected from the mud of a shallow temporary pool near the City Reservoir, March 8, 1939. Both specimens were very sluggish and were apparently moving toward the lake from their winter retreat in the shallow pool. Both were males with enlarged testicles and vas deferens swollen with motile sperm. Intestinal tracts were empty.

The growing season of these turtles in southern Illinois begins about the first of May. Thus, assuming no growth after the turtles enter the water in the fall (which is indicated by the size of hatchlings collected in March and April) and if the average carapace length of 54 hatchlings may be used as

an indication of size at hatching, first season turtles collected in June and July had grown as indicated in this chart.

Observation on First Season Growth in *Chelydra*

Date Collected	Locality	Cl.	Av. Cl. of 54 hatchlings	Growth from May 1 to date collected
June 5, 1939	Pond, Sesser	4.70	3.01	0.69 cm.
June 30, 1940	Carbondale City Reservoir	3.58	3.01	0.57 cm.
June 30, 1940	Herrin Lake	4.40	3.01	1.39 cm.
July 9, 1940	State Pond	4.01	3.01	1.00 cm.
July 9, 1940	State Pond	4.20	3.01	1.19 cm.
July 9, 1940	State Pond	3.92	3.01	0.91 cm.
C.A.S.—1515; S.I.N.U.—33, 43, 544, 545, 321, 172, 110, 380.				

63. *Terrapene carolina* (Linné).—This box turtle is abundant in the flood plains and the creek valleys. During the wet season they wander far from these areas but return as the summer progresses and the land becomes dryer. Thus in late summer and fall the populations are concentrated in the creek valleys where the turtles seek protection and moisture by burrowing under logs and the thick layers of leaf mold. Fungi are abundant in these areas and the turtles apparently find them their choicest food.

A large female was observed Sept. 6, 1938 feeding on an oyster mushroom. Other fungi in the creek valley had been nibbled by the turtles. When the female was examined in the laboratory her stomach contained large chunks of mushroom, one beetle, wing covers and legs of several other beetles. The stomachs of three other turtles collected at the same time contained the following material:

Stomach 1. Small crayfish; 1 jawbone of Microtus; many pieces of grass.

Stomach 2. One large cutworm.

Stomach 3. Many pieces of grass; 2 cicadas.

Copulating pairs were observed April 20, 1939 in Indian Creek valley and near the Big Muddy River north of Carbondale Sept. 12, 1939. The eggs are laid in a shaallow hole during the last of May or the first week of June. A specimen collected May 27, 1939 near Carbondale, contained 5 eggs ready to be deposited. Another collected June 6, 1940 contained two eggs with well calcified shells.

Although this turtle is usually considered entirely terrestrial, it enters the shallow waters frequently. Many specimens were collected as they rested half-buried in the mud about the margins of lakes and streams. On two occasions turtles were observed in several feet of water.

On June 6, 1939 a turtle was observed crawling about on the bottom of a clear water, clay bottomed stream leading to the Carbondale city reservoir. When first observed, it was under one foot of water and was moving upward toward the bank. Startled at the sight of the observer it retreated to deeper water, walking on the bottom.

In May, 1938 a specimen was collected from its resting position on the rock bottom of Bradshaw Creek. It was in water about one foot deep. S.I.N.U. —41, 42, 293, 294, 296, 299, 300, 301, 305, 309, 311, 313, 314, 315.

64. *Terrapene ornata* (Agassiz).—Two specimens were observed in a collection made by students of Royalton High School. They were collected in the immediate vicinity of the town but specific data was not available. There are some sandy soil areas in north eastern Jackson county that probably support an *ornata* population.

65. *Chrysemys picta* ssp.—The great majority of the *Chrysemys* collected are intergrades between *Chrysemys picta marginata* and *Chrysemys picta bellii*. Other specimens appear to be intergrades of one or both of these forms with *Chrysemys picta dorsalis*. Sufficient specimens have been collected to provide data for a partial solution of the *Chrysemys* problem in this region. A careful analysis of this situation will be presented in a forthcoming publication.

Although a considerable mass of ecological notes are available for *Chrysemys picta* they will not be presented until the taxonomic problem becomes clarified.

66. *Pseudemys scripta elegans* (Holbrook).—Abundant in creeks, ponds, and lakes. Its life cycle is being studied in detail and will be published when sufficient data is available.

67. *Graptemys geographica* (Le Sueur).—Found only in the larger streams and rarely in the larger lakes. A.M.N.H.—46493.

68. *Graptemys pseudogeographica pseudogeographica* (Gray).—Abundant in the Big Muddy and Mississippi Rivers. Observed rarely in the lakes. A.M.N.H.—4748-49.

69. *Amyda mutica* (Le Sueur).—Abundant in the larger rivers and creeks. A.M.N.H.—46494. U.M.Z.—81570.

70. *Amyda spinifera* (Le Sueur).—Abundant in the larger rivers and creeks. A.M.N.H.—46495; U.S.N.M.—55680-81; F.M.N.H.—18623.

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Another Case of Species Versus Subspecies

Hobart M. Smith

Herpetological and systematic literature has recently been augmented by the appearance of a very admirable revision and summary of "The Long-Nosed Snakes of the Genus Rhinocheilus" (Trans. San Diego Soc. Nat. Hist., vol. 9, No. 29, 1941, pp. 289-332, pls. 12-13, map) from the prolific pen of Laurence M. Klauber. The work mentioned was completed with no less painstakingly accurate care than usual in Klauber's studies; in fact only because of this thoroughness was the study brought to a satisfactory conclusion. More than one other author in recent years has given up a study of this genus with its seemingly meaningless complexity of variation of many types.

The genus includes certain forms occurring in Mexico, the herpetological fauna of which has been a subject of my interest for some time, and accordingly I have had more than casual reason for examining Klauber's arrangement of species and subspecies. Only through a different manner of interpretation of his data can I suggest a certain change in the arrangement he proposes.

The map reproduced herewith from Klauber's paper shows the distribution of the four forms of the genus, all of which he concludes represent subspecies of a single species. Two of the subspecies *(antonii* and *tessellatus)* are geographically distinct, while two others *(clarus* and *lecontei)* overlap so extensively both geographically and ecologically (at least no ecological segregation is yet apparent) that the relation between them cannot be visualized as the usual territorial one. As Klauber states (p. 320): "It may be suggested that these two forms were once territorially separated until they had become distinct, but have not recontacted and are spreading through each other's territories, without completely merging into an intermediate pattern." This is a very plausible—in fact almost inevitable—conclusion if the "geographic" or "territorially distinct" theory is assumed to account for the evolution of these two races. This theory is, of course, almost universally accepted as an explanation of most speciation in animals. On the contrary, however, *clarus* and *lecontei may* have become differentiated in at least one other fashion—by some type of "DeVriesian" mutation. In the latter case, admittedly of very little potential occurrence, the newly-formed species may, and presumably usually does, spread through part or all of the range of the parent species, but on the other hand it may, of course, occupy a territorially distinct area, providing conditions (both intrinsic and extrinsic) permit. Accordingly, either Klauber's explanation or the "DeVriesian" mutation theory may account for the curious association of *clarus* and *lecontei.*

If the mutation theory were assumed to furnish the correct explanation in the case under discussion, the relation of *clarus* and *lecontei* can be considered to depend upon two considerations. *First,* there may be a more or less complete "protoplasmic" continuity of the whole *Rhinocheilus* population of the total area inhabited by the two racial types (in other words, a total, or nearly

complete, lack of isolation from the parent type of the possessor of the genetic change), and in such case the characters of one (the new) racial type (presumably *clarus*) must obviously be spreading throughout the whole population of the area. *Second,* any one of several types of isolation may accompany the characters used to define each racial type. If the *first* situation were true, the whole *Rhinocheilus* population must be considered as a single form; the only exception would be in case the new characters should have a strong selective value and also spread so uniformly from a central point that the populations carrying them could be differentiated geographically as well as morphologically from the remaining populations. In such exceptions the use of sub-specific names could be recommended, but clearly the *Rhinocheilus* racial types in question are not among these exceptions, since the presumably new, variant type *(clarus)* is scattered irregularly throughout nearly a half the total range of the parent *(lecontei)* racial type; both occur at the same locus. But if the *second* situation were true, the two types must be considered as belonging to distinct species; for various reasons sufficiently evident, I believe this situation is the true one, *if* the mutation theory is correct.

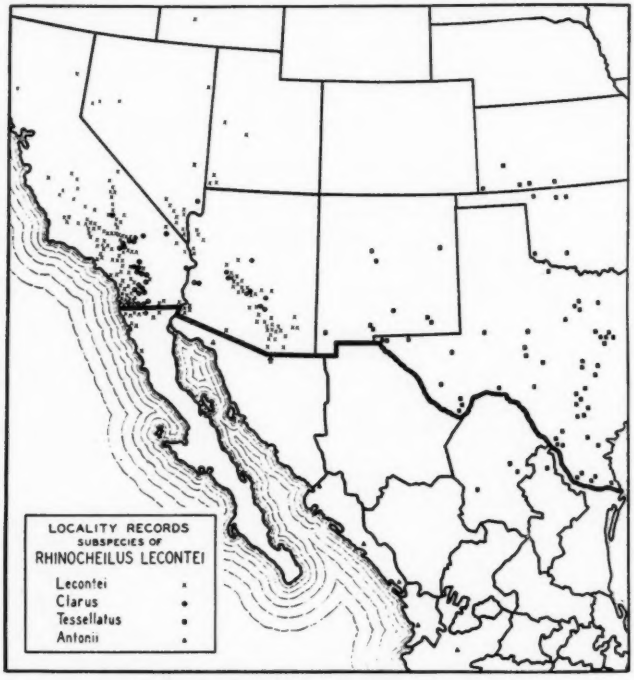

Fig. 1. The distribution of *Rhinocheilus,* from Klauber.

On the other hand, if Klauber's theory is correct (by far the more probable) the relation of *clarus* and *lecontei* may be considered to depend upon the extent of crossing or hybridization taking place between the two racial types. The forms *must* have been sufficiently well differentiated so that interbreeding was largely if not entirely inhibited, else upon coalescence the characters would merge completely and uniformly. It seems obvious, however, that if an actual blending of two previously distinct species is occurring, the transition is not from a specific status of each form toward a sub-specific status, but rather toward a complete loss of practical identification and separation. In other words, according to Klauber's theory, the two types must either be considered distinct species (the "intergrades" as hybrids) or else they cannot be considered distinct at all. There is no intermediate choice which would permit the use of the term "subspecies." The extent of hybridization in the present case is low, so it is practical to regard the two types, *clarus* and *lecontei*, as distinct species; but in other cases the extent of hybridization may be so great that it is impractical to recognize by name the variant types occurring. Klauber shows very clearly that separation of the two racial types in southwestern United States *is* practical, and therefore, by his theory, it must be concluded that we are dealing with two distinct species, occasionally hybridizing. The point at which the line between recognition and non-recognition may be drawn is to some extent a matter of personal opinion, and may be worked out by various methods. In this particular case there is little doubt.

In summary, it may be stated that whether *clarus* and *lecontei* have become differentiated by territorial isolation or by some type of "DeVriesian" mutation, by either theory the two forms in question must be considered as distinct species. It must therefore be concluded that the forms of *Rhinocheilus* should stand as:

Rhinocheilus lecontei lecontei Baird and Girard 1853.
Rhinocheilus lecontei tessellatus Garman 1883.
Rhinocheilus antonii antonii Dugès 1886.
Rhinocheilus antonii clarus Klauber 1941.

Only if (1) an ecological segregation of *clarus* and *lecontei*, with intergradation occurring in the areas where the two types of ecological conditions merge; or if (2) intergradation between *antonii* and *tessellatus* across the Sierra Madre Occidental of Mexico (thus forming a complete intergrading series from *clarus* through *antonii*, *tessellatus* and *lecontei*) can be proved, will it seem reasonable to consider *clarus* and *lecontei* subspecies of the same species.

Commenting upon the view presented here, Klauber (in letter) states: "Of course, I knew when I recognized *clarus* as a valid subspecies of *lecontei* that the peculiar geographical situation would lead to considerable comment, and some disagreement. . . . It seems to me that if there is any one argument that might be used against your view, it is the number of intergrades in almost every degree of intergradation that occur around the periphery of the most typical *clarus* area, namely, that of the Borego and Coachella valleys."

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Life History Studies of the Cottontail Rabbit in Southwestern Michigan[1]

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The cottontail rabbit is one of the most important game animals in the United States, yet little effort heretofore has been made to determine the habitat requirements and to develop management measures for this species. The two most extensive studies of this nature to date have been those of Trippensee (1934) and Allen (1938a). When we consider that the annual kill of cottontails in Michigan alone is over 2,000,000 individuals, it becomes apparent that this species is worthy of detailed investigation to formulate a basis for sound management. The huge numbers of cottontails imported by various eastern states for planting prove that those states were in need of better methods for properly managing their native cottontail populations.

The present study was initiated in January, 1938, and terminated in December of 1939. Information here presented represents part of the data collected while studying the effects of various proposed management masures on populations of the cottontail *(Sylvilagus floridanus mearnsii)*.

Grateful acknowledgement is made to the Michigan Department of Conservation for providing the part-time fellowship and other support which made this study possible. The encouragement and advice of H. D. Ruhl, chief of the Game Division is appreciated. Dr. Lee R. Dice of the University of Michigan directed the studies. Dr. W. H. Burt of the University of Michigan has given many helpful suggestions. Dr. D. L. Allen, then Biologist in charge at the Swan Creek Wildlife Experiment Station, contributed many field records and valuable field supervision. The United States Department of Agriculture and Works Progress Administration did considerable developmental work on the study areas. The cooperation of F. J. Hodge, then in charge of the wildlife developmental work for the United States Department of Agriculture, is appreciated.

Betty M. Robertson of the University of Michigan Department of Botany identified the plants collected during the study. Identification of several parasites has been made by Dr. J. C. Bequaert of Harvard University, Dr. H. E. Ewing of the United States Bureau of Entomology, and Drs. S. C. Whitlock and Carl Gower of the Michigan Department of Conservation Pathology Laboratory. Many valuable field records were contributed by F. W. Stuewer, R. C. Dunning, P. S. Baumgrass, J. D. Cameron, and W. T. McConnell.

Area Studied

The major portion of the present study was made on parts of 10 sections of land on or near the Swan Creek Wildlife Experiment Station, Allegan County, Michigan. These sections were 5, 8, 9, 17, 21 and 28 of Valley Township, sections 31 and 32 of Heath Township, and sections 11 and 12 of Clyde

[1] Extraction from a dissertation submitted in partial fulfillment of the requirement for the degree of Doctor of Philosophy, in the University of Michigan.

Township, all of Allegan County, Michigan. The major portions of the investigation were made in upland habitats which lie within half a mile of fertile lowland areas. Many records, however, were secured in riverbottom habitats.

PHYSIOGRAPHY AND SOIL

The surface area is generally flat (650 feet above sea level), with only a few minor irregularities. The Kalamazoo River cuts through the sandy upland plain in the form of a wide meandering valley with extensive bayous. Abrupt escarpments which rise up to 50 or 60 feet in a few places separate the upland from the riverbottoms.

The soil consists of Plainfield Sand (formerly known as "Allegan Sand") which is very deep, sections of 30 to 60 feet being recorded (Fippin and Rice, 1901). Only a small amount of organic matter is found in the thin sandy loam surface layer of soil. According to Veatch (1933), the land is of third class, which is in general submarginal, or locally marginal.

CLIMATE

The annual precipitation in Allegan County is about 30 inches. Included in this amount is an annual snowfall of 60 inches (Fippin and Rice, 1901). The mean temperature for the county is about 48 degrees Fahrenheit, the average annual maximum 95.9 degrees, and the average annual minimum minus 12.1 degrees Fahrenheit. The average length of the crop growing season is about 160 days (Leverett, 1917). During 1938 and 1939 the weather was not unusual.

VEGETATION

The present woody vegetation on the sandy upland plains consists almost entirely of oaks *(Quercus alba* and *Quercus velutina)* ranging in size up to about 10 inches in diameter at breast height. A moderate amount of sassafras, cherry, and dogwood is found amongst the smaller ground cover. The deserted farm lands are slowly being invaded by weeds, dewberry, sassafras, cherry, and oak. A few of the old fields, however, have large patches of "blow sand" which have been partially put under control by soil conservation measures.

With the advent of fall frosts, the leaves of most shrubs and trees are dropped. Most white oaks and much of the black oak coppice and reproduction, however, do not drop their leaves until after the snow has disappeared the following spring (Fig. 1).

OCCURRENCE OF HOLLOW TREES AND BURROWS ON UPLAND

A few (about 1 per 20 acres) of the oak trees on the areas have small hollows in their bases. Such holes, where they occur, are readily used by rabbits. Hollow pine logs are used occasionally, but their scarcity (about 1 per 40 acres) limits their usefulness. Woodchucks and skunks are seldom found on the upland, and accordingly, their burrows are usually lacking. A badger or family of badgers which were occupying one or more of the study areas, were not known to use more than three or four burrows. Apparently, the

Fig. 1. Good cottontail cover. Fig. 2. No rabbits were taken at this trap station during two years of study. No suitable cover for rabbits present. Fig. 3. One of the largest beds of cactus in the region. Fig. 4. Destruction of the natural cover caused this "sand blow," which is now healing over.

scarcity of ground squirrels provided little opportunity for badgers to dig in pursuit of such prey. A few of the upland sites are lacking in suitable winter cover (burrows, brush piles, coppice) and consequently the rabbits migrate from those areas into the bottomland during that season (Fig. 2).

Methods of Study

Information about the cottontail has been secured by live-trapping, shooting, examining dead individuals from roads, examining burrows, tracking, scatology, and direct observation.

TRAPPING TECHNIQUE

Spacing of traps.—Forty-nine permanent trap stations were established in each of the six 160-acre areas studied. These trap stations were located at 110-yard intervals and arranged in a grid pattern. Outside rows of traps were located 110 yards inside the border of the areas. Trap stations were numbered in consecutive order, and a metal tag stamped with the quadrat and trap station number was nailed to a nearby tree or post.

Each of the traps was set near the most suitable cover available within 50 feet of the established station. The most suitable place was usually at the base of a clump of bushes or near the base of a tree. Traps were usually placed with their entrance directed toward cover. During summer, traps were placed where they would be shaded during the forenoon, because continued exposure to hot summer sunshine is fatal to cottontails.

Traps.—A trap similar to the "Evans vermin trap" (McAtee, 1930, Fig. 2) has been effective for live-trapping cottontails. A suitable size for such a trap is 12 inches high, 12 inches wide, and 24 inches long.

Baits.—A combination of plain ear corn, or corn soaked for 2 or 3 days in a salt solution, and rolled oats or apples has proved to be effective bait for cottontails. Combinations of these baits have attracted rabbits at all seasons. A large number of additional baits were tried at times, but these did not show any promising results. These additional baits tried were commercial cow feed, whole oats, scratch feed, commercial rabbit pellets, alfalfa, shredded Ralston cereal, carrot, radish, turnip, beet, parsnip, raisins, catnip, pennyroyal, mint, and vanilla. Smoked herring was often placed along with other baits in the traps in order that the catch of raccoons might be increased.

Cottontails do not react in the same manner to baits at all times. One night the rabbits may run directly past a trap without hesitation. On another night, they may pack the snow down all around the trap, but will not enter. At still other times, they enter the traps freely.

Tending traps.—Traps were visited during the forenoon of each day. Whenever two or more traplines were operated simultaneously, some traps could not be visited until about noon.

Handling rabbits.—Rabbits were removed from traps in the following way: the trap was set on end, then the operator reached into the trap and seized the rabbit from above. The struggles of the rabbit were least successful when it was seized about the neck with the thumb and index finger, and the little finger hooked around the hind foot, which was then brought forward (Fig. 5). When a rabbit was held thus, it made little attempt to kick with the other hind leg, and was never injured. The rabbit was then placed into a small cloth bag where it was examined for sex, age, ectoparasites, and general condition, its hind foot and ears measured, and its weight taken. If the rabbit was an adult female, it was examined for signs of lactation and pregnancy. Measurements were taken of the length of testes of males. Rabbits which were taken for the first time were marked by attaching consecutively numbered tags to their ears. Males were tagged on the right ear and females on the left. The tag numbers of rabbits which had been marked previously were recorded with the other data taken.

During summer and fall of 1939, rabbits were tagged in both ears as an insurance against loss of identity with loss of ear tags. Both button type and fingerling tags were used (Figs. 6 and 7). Fifteen tags were known to have been lost during 1938 and 1939. Apparently, both types of tags are sometimes torn from the ear. The fingerling tag is probably the least susceptible to loss if properly attached to the ear. The most satisfactory way to attach fingerling tags to a rabbit's ear is to insert it through the back side of the ear at 2 places arranged in a proximal-distal direction (parallel to axis of ear, Fig. 7).

Tracking.—Tracking in a fresh snow has proved to be an excellent means of determining the range of activity of rabbits. The extent of use of artificial food, artificial burrows, and brush piles has been effectively determined by tracking. On several occasions, tracking showed the absence of cottontail activ-

Fig. 5. A safe, painless, and easy way to handle a cottontail. Fig. 6. A cottontail which has been marked with a numbered button-type ear-tag in each ear. Fig. 7. Cottontail marked with numbered fingerling-type ear-tag. Photo by L. C. Hulbert.

ity in one area, when an abundance of rabbit activity was found in more suitable areas.

On a few occasions, a colored paste prepared from methlyn blue, glycerine, and flour was smeared on the feet of live-trapped rabbits. The color left in the tracks served as an aid in tracing range of activity. The preparation rapidly lost its value for coloring the foot prints, but did last for 12 hours if the snow was wet.

Scatology.—The fecal pellets of rabbits serve as an index to the use of brush piles. The presence of large numbers of fecal pellets along the perimeter of brush piles indicates that cottontails spend considerable time sitting in the edge of such cover. In late winter of 1938, one large brush pile contained an average of 48 fecal pellets per foot of perimeter, or edge of the pile. Several nearby brush heaps were used almost as intensively.

Various harmless stains were given to a few rabbits to color the feces and urine. The colored urine and fecal pellets were then used as clues in studying the home range of individuals treated. Blackish pills resulted from the forced feeding of charcoal. Methlyn blue colored the pills green, and the urine a bluish green. Reddish saffranin colored the urine reddish, and the pellets a pinkish brown. Alphazurine stained the pills a brilliant green color which was recognizable at a distance of 8 to 10 feet. Gentian violet and acriflavine stains were unsatisfactory. These stains were administered by placing them in small gelatine capsules which were then forced down the throat of the rabbits.

Life History

A sound management plan for any species must consider its needs as exhibited by its everyday habits and life processes. Accordingly, I have endeavored at all times to gather all available information relative to the life history of the cottontail.

General Behavior

Fear.—Cottontails lose some of their fear of man when they are recaptured frequently. The first time they are taken, they usually batter themselves against the wire of the trap. On subsequent captures, however, they remain more quiet at the approach of the operator. A few rabbits which were brought into close proximity with weasels, skunks, and opossums did not show much fear until attacked. If the attack occurred in a burrow, as described elsewhere in this paper, the immediate reaction was to dash from the burrow, even when the only exit was past the attacker. Captive rabbits, however, were much frightened at the approach of a dog.

Defense.—A mature rabbit is far from defenseless. Its powerful hind legs are deadly weapons. During the first year of study, the writer's hands were constantly scratched until he learned how to seize and hold a rabbit properly (Fig. 5). Captive rabbits proved to be especially difficult to handle. When an attempt was made to grab them, they usually attempted to elude capture, but when cornered they became aggressive and fought. These captives defended

themselves by stabbing with the front feet, and then suddenly lashing forward with both hind feet. When confined in a bag, they would sometimes bite. One rabbit when attacked by a skunk in a burrow seemed to lie back on the dorsal part of its rump and to thrash the skunk with its powerful hind legs.

Voice.—Ordinarily, a rabbit does not use its voice, but when seized and lifted into the air, it may utter a high-pitched rasping sound. On a few occasions, while young rabbits were being taken from a nest, they uttered this call. The other young left the nest immediately and scattered, so the call in this case served as an alarm.

Sociology.—Eight pairs of rabbits were kept in small pens (3 x 5.5 feet) during the summer and fall of 1939. The claws of one pair, which fought considerably during their first night together, were cut short and blunt. No serious fighting occurred after this treatment, and no fatalities occurred. Some of these rabbits had been reared in captivity, while others were taken from the wild. Several wild-caught rabbits have been kept over night in a single compartment without fatalities. These wild rabbits seemed more tolerant toward each other than cottontails are usually reported to be.

Rabbits have on several occasions been taken in pairs at a single station during the breeding season, when two traps were operated at the stations. This apparent companionship was evidently due to sexual instincts.

On one occasion an adult male in breeding condition was taken in the same trap with an immature female which weighed only 14 ounces. Perhaps then there is some companionship between juvenile and adult rabbits.

WINTER FOOD ON UPLAND

During the winter, cottontails occupying the sandy upland usually made use of the foods which were most available. Bark, twigs, and buds of white oak,

TABLE 1.—Plants used for food by cottontails on upland study areas, during winters of 1937-38 and 1938-39. Listed in order of importance as food.

SPECIES	AVAILABILITY	USE
Quercus alba (White oak)	abundant	frequent
Cornus florida (Flowering dogwood)	common	frequent
Sassafras albidum (Sassafras)	common	frequent
Quercus velutina (Black oak)	common	frequent
Ceanothus americanus (New Jersey tea)	common	frequent
Pinus Strobus (White pine)	common	less frequent
Smilax sp. (Greenbrier)	occasional	less frequent
Rubus procumbens (Dewberry)	abundant	less frequent
Pyrus malus (Apple)	occasional	less frequent
Pinus Strobus (White pine)	occasional	infrequent
Vaccinium sp. (Blueberry)	occasional	infrequent
Crataegus sp. (Hawthorn)	occasional	infrequent
Populus alba (Silver-leaved poplar)	scarce	infrequent
Rosa sp. (Rose)	occasional	infrequent
Artemisia caudata (Wormwood)	abundant	infrequent
Gaylussacia baccata (Huckleberry)	occasional	infrequent
Gaultheria procumbens (Teaberry)	local	infrequent
Hamamelis virginiana (Witch-hazel)	common	infrequent

flowering dogwood, sassafras, and New Jersey tea were taken in liberal amounts in the order listed (Table 1). Black oak was similarly used, but the buds were cut from the twigs and rejected. It was rather common to find a group of black oak buds lying where a rabbit had been feeding on the twigs of that species. Wormwood *(Artemisia caudata)* which grows in abundance on the areas was apparently not taken for food as frequently as its availability permitted. Wild black cherry, greenbrier, dewberry, and apple, were used only in moderate amounts. Lack of availability was probably the limiting factor in the infrequent use for food of such plants as white pine, blueberry, hawthorn, silver-leaved poplar, rose, huckleberry, teaberry, and witch-hazel.

The list of foods used by the cottontails (Table 1) is not intended to represent all foods taken on the upland during winter. However, it does contain all important foods, as well as a few lesser important ones.

REPRODUCTION IN THE COTTONTAIL RABBIT

In spite of the fact that the cottontail rabbit is one of our most important game species, accurate information relating to its breeding season has been inadequate. Data relating to the breeding of this animal seem to have been chiefly secured through autopsies, from the absence or presence of signs of lactation in dead females, nests of young, and from observations on mating behavior. Trippensee (1934) noted the annual increase and decrease in size of testes in the males, the presence of embryos in autopsied females, and nesting habits, and deduced from this evidence the breeding season.

This method of approaching the problem is undoubtedly sound, except that the amount of evidence to be secured by such a means is obviously limited, because the season for legal take is usually closed when the rabbits are breeding, and the nests are almost invariably discovered by accident. Beule (1940), however, has had considerable success at finding nests by a systematic search. Only one of the eight nests examined by me was found by intentional search.

Method of securing data on reproduction.—The present study differs from those of the past in that, in addition to nest and autopsy data, living wild female rabbits were periodically examined for signs of pregnancy or lactation, and males for size of testes.

Diagnosis of pregnancy.—The presence of uterine swellings, or large embryos in a living female cottontail was determined by gently pinching the walls of its abdomen together between the thumb, index, and second fingers. If the investigator is careful, fecal pellets, kidneys, uterine swellings, and occasionally a dilated bladder can be distinguished. Until one has had some practice with this technique, he may confuse parts of the rabbit's internal anatomy. However, with a moderate amount of effort and patience, he soon learns to diagnose a case of pregnancy which is sufficiently advanced to show uterine enlargements. Obviously, swellings of the uterus cannot be measured, therefore, they were classified as approximately the average size of a (1) cottontail fecal pellet, (2) hazelnut, (3) hickory nut, (4) or walnut. Swellings larger than a walnut were considered as evidence of an advanced stage of pregnancy. Preg-

nancies in which the uterine swellings were approximately the size of a fecal pellet usually were questioned, and later verified when the rabbit was recaught and found to have uterine swellings of increased size.

The age of one embryo which was secured from a 14-mm. uterine swelling in a wild cottontail has been determined by Dr. A. H. Stockard, of the University of Michigan, to be about 12 days. Such a uterine swelling (14-mm.) when palpated in the abdomen of a live rabbit feels comparable in size to a large hazelnut.

Measuring testes.—The method used for measuring the combined lengths of a testis plus its epididymus, while still in the scrotum of a living rabbit, was to gently force the testis into the bottom of the scrotal sac by means of the thumb, index, and second finger of the left hand, and then measure the organ with a 6-inch ruler held in the right hand. This procedure can be employed with a minimum of struggle on the part of the rabbit, if its hind quarters are protruding from a closely fitting cloth bag, while the rabbit is lying on its back, head facing the left, on the lap of the observer. Since only a close approximation of the actual size of testes could be obtained by this method, the measurements were read to the nearest one-fourth inch, except in those instances where the measurements fell exactly on a one-eighth inch mark.

The testes of dead rabbits were removed from the animal before being measured. Only a single measurement was taken, the maximum length of the testis, exclusive of the part covered by the epididymus.

Gestation.—Dice (1929, 1933) found that an experimental mating of a pair of rabbits *(Sylvilagus f. alacer)* in captivity produced a litter of three young, which were found on the 28th day after mating, but explains that the litter may have been present before he found them. Hammond (1931) has found in the "domestic rabbit" that ". . . the mean duration of pregnancies is very slightly under 32 days, and that 95 per cent of the pregnancies lie between 30 and 34 days."

Evidence on length of gestation period in wild cottontails.—Eleven females were handled repeatedly in one quadrat during the breeding season of 1939. Four of these were retaken at times when they were apparently undergoing a subsequent gestation period with embryos comparable in size to those observed in an immediately previous pregnancy of the season. One of these females was found in the advanced stages of three separate pregnancies during the 1939 season. The number of days which elapsed between apparently similar stages of development in successive pregnancies of individual females are presented in Table 2. Female No. 17 was taken twice, 34 days apart, and contained advanced embryos of about equal size on these occasions. Thirty-one and 32 days after rabbit No. 941 was observed in an advanced stage of pregnancy, she was found to have uterine swellings of walnut size, and on the 67th day she was again in an advanced stage of pregnancy. This female, therefore, must have completed gestation of the embryos which were of walnut size, and barring abortion, must have given birth to her young, again become pregnant, and undergone gestation of a succeeding litter (2nd) to an advanced stage, all in

a period of 35 days. A third female (No. 946) showed two advanced stages of pregnancy only 26 days apart. On June 15 and 17, and again on July 14, female No. 61 was recorded as pregnant with embryos about the size of a walnut. The minimum time between handling this female was 27 days, and the maximum time 29 days. A female handled repeatedly on another area required 19 days for its uterine swellings of hazelnut-size to develop into embryos which would probably be born within a day or two.

TABLE 2.—Time Interval Between Comparable Stages of Succeeding Pregnancies of Individual Female Cottontail Rabbits.

Animal Number	Date of original observation	Days until succeeding comparable size of embryos	Days until third comparable size of embryos
17	May 20	34	....
61	June 15	27–29	....
941	April 24	....	67
946	May 2	26	....
Average No. days interval		29.3	67

It is recognized that the time between the various designated stages of pregnancy is probably not constant, and that a diagnosis of a given stage of pregnancy is only an approximation, which may vary 4 or 5 days in its accuracy. However, female No. 941 more than completed the cycle from one litter to the next in 35 days. The gestation period for this species is therefore less than 35 days, and may be as low as 26 days. Hammond and Marshall (1925) found that "while it is a rule in the rabbit that pregnancy does not occur during lactation, there are two circumstances under which it is possible: (a) where only a small number of young are being suckled, and (b) in times of abundant nutrition suitable for breeding." Vorhies and Taylor (1933) in working with *Lepus alleni* and *L. californicus* found that "pregnancies frequently occur while young are being suckled. . . ." Therefore, if copulation and resultant fertilization follows parturition immediately, then the gestation period of *Sylvilagus f. mearnsii* is less than 35 days and probably more than the indicated 26 days minimum. Gerstell (1937b) found in captive rabbits ". . . that births occurred any time between 25 and 32 days after copulation, the normal period of gestation apparently being 30 days." Some variation in length of the gestation period is to be expected. Hammond and Marshall (1925) observed that the duration of 95 per cent of the pregnancies in the domestic rabbit did not vary more than 4 days, and that ". . . there is only a suggestion that the duration of pregnancy, when it occurs, has been slightly prolonged by increasing the number of young suckling; the limits, however, do not exceed the normal variation."

The average length of time between comparable stages of pregnancies in a single female, as based on evidence from four individuals, is 29.3 days. The average gestation period is, therefore, probably about 29 or 30 days.

Number of litters.—Dice (1929, 1933) succeeded in rearing, in one season, two litters of young from a pair of captive rabbits *(Sylvilagus f. alacer)*. Trip-

pensee (1936) states that "no direct evidence has been obtained on the number of litters in southern Michigan." Allen (1938b) says, "If the gestation period of the cottontail is roughly one month and the young are cared for by the mother for 16 (or a few more) days, 50 days would encompass the length of time needed for producing a litter." On the basis of this calculation, Allen indicates that probably only two litters are ordinarily produced in a season.

Evidence on number of litters borne during one season.—The number of litters an individual female cottontail may bear during a single season has been determined for five females (Table 3). These females were recaptured frequently during the intensive study of a sample area (160 acres) in 1939. Intensive trapping operations within this area were conducted as follows: April 13-May 6, May 24-29, June 27-July 3, and from August 5 to September 18, 1939. Nine adult females were taken during April 13 to May 6. Some females were not retaken during subsequent censuses, others were not recaught until the third or fourth recensus was taken. Only two additional individual females were taken as the season progressed.

If the mammae of a rabbit contained milk, or if the hair about the nipples

TABLE 3.—Frequency of Pregnancies Among Female Cottontails Taken on a Sample Area.

Date		Female number										
		17	134	163	491	500	504	821	941	946	951	1011
April	1-10	..	..	..	..	..	..	..	..	..	..	..
	11-20	L1	L1	A1	L1	P1	..	L1	L1F2	A1	..	..
	21-30	Hc2	Hc2	..	..	..	..	..	A2	..	F1	..
May	1-10	..	..	..	..	..	L1Hz2	..	..	Hc2	L1	..
	11-20	..	..	..	..	..	..	..	..	..	..	..
	21-31	A3	W3	F2	..	..	F3	..	W3	Hz3	..	L1A2
June	1-10	..	..	..	..	..	..	..	..	..	..	..
	11-20	..	..	..	..	..	..	..	..	..	..	..
	21-30	A4	..	..	..	..	Hz4	..	A4	..	..	..
July	1-10	..	..	..	..	..	..	..	..	..	..	..
	11-20	..	..	..	..	..	..	..	..	..	..	..
	21-31	..	..	..	..	..	L	..	..	..	..	..
August	1-10	..	..	..	..	..	..	..	..	..	..	L
	11-20	..	..	..	..	..	..	..	L	..	..	LHz3
	21-31	..	..	..	..	L2	L	..	..	L4	..	..
Sept.	1-10	..	..	..	..	..	L	..	..	..	..	..
	11-20	..	..	..	..	..	..	..	..	..	..	..
	21-31	..	..	..	..	..	..	..	..	..	..	..
Apparent no. times pregnant		4	3	2	1	2	4	1	4	4	1	3

Key: Sizes of Pregnancies—1, 2, 3, 4,—first, second, third or fourth pregnancy
F—fecal pellet
Hz—hazelnut
Hc—hickorynut
W—walnut
A—advance
P—size unknown — no observation
L—lactating (at least 1 litter born)

was matted when examined, it was considered that the rabbit had given birth to a litter. Hammond (1931) found in the domestic rabbit that "from about the 20th day onwards the mammary gland begins to undergo its thickening or alveolar glands stage of growth (felt as a thickening when the skin is held between the finger and thumb—an indication of pregnancy)." Until the time when such a change in the mammary glands takes place, it is reasonable to suppose that a rabbit cannot lactate. Therefore, a rabbit found lactating, and at the same time carrying embryos no larger than a walnut, was considered to be in at least its second pregnancy for the season.

It is evident that if an individual was handled approximately once each month, the number of pregnancies during a single season could be determined. Trapping on the sample area was not begun, however, until about a month after the advent of the breeding season.

Five of the females examined had apparently completed their first pregnancy of the season prior to the middle of April, as they were lactating at the time (Table 3). Three of the 11 does handled on the sample area during the breeding season, were apparently pregnant once; 2, twice; 2, three times; and, 4, 4 times. Two of the three which were found pregnant only once, were not retaken, and hence are not completely accounted for. The third female (No. 821) with only one observed pregnancy, was repeatedly retaken on a distant area during July. She was neither pregnant nor lactating. This female should probably not be considered as normal because she was "stocked" onto an adjoining area on January 26, 1939. At that time she was released in an unoccupied locality where a female of the same age had perished. However, she seemed inclined to roam, with no apparent fixed home range. Both animals which were twice found pregnant were not retaken a sufficient number of times to allow a determination of the complete number of pregnancies. Each had ample time to breed three or even four times during the season. Female No. 500, which was found pregnant in April, was not retaken until late August at which time she was lactating. Therefore, it seems reasonable to assume that she had given birth to at least two litters during the season. Rabbit No. 134, which in late May was pregnant for the third time, was not retaken thereafter.

Under favorable conditions, pregnancy does occur in the "domestic rabbit" during lactation (Hammond and Marshall, 1925). They likewise found that a high percentage of fertile coitions occurs during the first four days after parturition. Vorhies and Taylor (1933) found that in the jack rabbit *Lepus alleni* and *L. californicus*, "pregnancies frequently occur while young are being suckled. . . ." In general then, it seems that the four pregnancies indicated by four of the 11 females taken on this sample area were not unusual for the region.

None of the rabbits handled were found pregnant during the same year in which they were born. Females of *Sylvilagus audubonii audubonii*, however, do mature and bear young during the same year (Ingles, 1941).

Testes.—Trippensee (1934) found that the size of the cottontail testes began to increase in early December, reached a maximum in April, and was

sharply reduced during the latter part of July and August. His findings are based on relatively few measurements, most of which were evidently taken during late fall months. Early in the present study, it was realized that if a series of seasonal measurements could be taken on the testes of a single individual, much could be learned about the duration of the reproductive season.

The testes (in scrotum of living rabbits) in 87 adult and 89 juvenile cottontails were measured a total of 246 and 143 times, respectively, during 1938 and 1939. In addition, 28 adult and 18 juvenile male rabbits were autopsied, and the testes measured after they were removed from the scrotum. This autopsy measurement is the distance from the opposite ends of the testis, excluding the part covered by the epididymus. Testes measured after they were removed from the scrotum have usually been of a size intermediate to the extremes of the sizes found by simultaneous measurements on a number of live rabbits. The apparently close correlation in sizes of testes found by the two non-comparable methods may be due to a slight compression of the testis and its epididymus as they are gently forced into the bottom of the scrotum to be measured. Size of testes as determined by periodical measurements on live rabbits, and from autopsies, have been grouped together to show the trend of seasonal changes in testis size of cottontails (Table 4).

Seasonal fluctuations in testis size of adults.—The testis size rapidly rises during January, February, and March, then increases more slowly to a high level in April and early May (Graph 1, Fig. 8). Decline in size is rather slow during June and most of July, but drops off rapidly in late July and August (Fig. 9). By the middle of September, the size of adult male testes has fallen to about 1.1 inch, at which size they apparently remain until December (Figs. 10 and 11). The decrease in average size to 1.0 inch during late October is only 0.1 inch smaller than the average for the other fall periods, and is probably not significant.

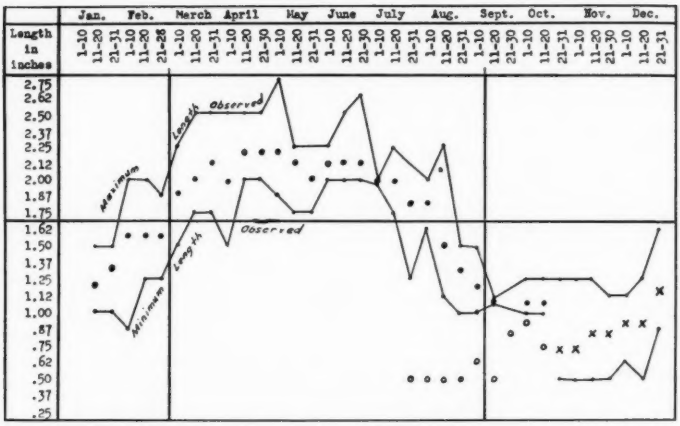
Increase of testis size in juvenile rabbits.—The testes of living juvenile rabbits cannot be measured in the scrotum satisfactorily until the animal is about a third grown, and then only with difficulty. Measurements of the testes of juvenile rabbits were first secured in July, at which time they averaged one-half inch in length. From this time on, the size of testes increased, with some apparent fluctuations, until mid-December, when they were 0.9 inch long. Until about October 21, juvenile and adult male cottontails could be distinguished on the basis of testis size (Fig. 11). From this time onward, however, a small amount of overlapping in range of sizes occurs. Therefore, after the middle of October, it is advisable to treat all males as one group of potential breeders. The average testis size for such a group is given in Table 4.

Breeding season.—Trippensee (1936) says, "Observations in the field indicate that there is a definite breeding season for the Mearns cottontail beginning in the middle of January and extending to the middle of August." Allen (1938b) states that the regular breeding season lasts from February through July, although some breeding evidently occurs earlier and later than this.

In my study, the rabbits examined prior to March 14 were apparently not

TABLE 4.—Summary of Data on Cottontail Rabbit Breeding Season, 1938, 1939.

Period of month by ten-day intervals	Males							Females		
	Adult			Juveniles				Adult		
	Mean length of testes in inches	Number individuals	Number measurements	Mean length of testes in inches	Number individuals	Number measurements	Mean length of testes in combined age classes	Individuals pregnant	Individuals lactating	Individuals not pregnant
Jan. 1-10	....	0	0					0	0	ALL
11-20	1.2	4	8					0	0	ALL
21-31	1.3	5	5					0	0	8
Feb. 1-10	1.6	16	20					0	0	6
11-20	1.6	13	22					0	0	2
21-28	1.6	6	10					0	0	1
Mar. 1-10	1.9	17	21					0	0	4
11-20	2.0	15	16					3	0	7
21-31	2.1	15	16					5	0	7
Apr. 1-10	2.0	11	12					4	0	2
11-20	2.2	17	22					12	13	2
21-30	2.2	5	5					4	7	2
May 1-10	2.2	7	9					4	10	1
11-20	2.1	12	14					9	9	0
21-31	2.0	6	6					14	15	3
June 1-10	2.1	2	2					4	4	0
11-20	2.1	6	7					6	10	1
21-30	2.1	8	10					3	10	3
July 1-10	2.0	1	1					1	3	2
11-20	2.0	2	2					4	4	11
21-31	1.8	13	22	0.5	1	1		9	17	10
Aug. 1-10	1.8	8	9	0.5	4	4		2	8	5
11-20	1.5	3	3	0.5	3	3		1	4	4
21-31	1.3	7	10	0.5	5	5		0	6	5
Sept. 1-10	1.2	2	4	0.6	6	7		0	9	11
11-20	1.1	1	1	0.5	5	6		0	2	1
21-30	....	0	0	0.8	3	4		0	0	ALL
Oct. 1-10	1.1	2	2	0.9	1	1		0	0	ALL
11-20	1.1	2	3	0.7	4	4		0	0	ALL
21-31	1.0	7	8	0.7	21	36	0.8	0	0	ALL
Nov. 1-10	1.1	3	3	0.7	28	28	0.7	0	0	ALL
11-20	1.1	4	4	0.8	26	32	0.8	0	0	ALL
21-30	1.1	2	2	0.8	10	15	0.8	0	0	ALL
Dec. 1-10	1.1	2	2	0.8	4	5	0.9	0	0	ALL
11-20	1.1	3	3	0.8	11	11	0.9	0	0	ALL
21-31	1.2	8	8	....	0	0	1.2	0	0	ALL



Graph 1. Annual change in length of cottontail rabbit testes. Curve based on data from Table 4. Key: • Average length of adult testes; o Average length of juvenile testes; × Average length of juvenile and adult testes.

pregnant. On March 14, 1939, however, three of the six females taken had small uterine enlargements. From this date on, pregnancies were frequent. Signs of lactation were first found on April 11. Evidence of breeding (pregnancies or lactation) was found throughout April, May, June and July. The last pregnancy of the season was found on August 11, at which time this female had uterine swellings about the size of a hazelnut. She was probably destined to bear young some time in late August or early September.

On September 12, 1939, a nest with young was reported to have been found by a farmer near Dorr, Michigan. The report was checked by me and the deserted nest located. At least three farmers saw the young, whose eyes were open, run from the nest when disturbed. Allen (1938b) found evidence indicating that the eyes of a litter under observation opened on the eleventh day, and that the young left the nest on the 16th day. It is accordingly probable that the young rabbits in the nest on September 12 were born some time between August 27 and September 1.

Evidence of lactation continued to be found until the middle of September. From this time on, all females examined were without signs of either lactation or pregnancy (Table 4).

The term "breeding season" as used here refers to the length of time between the first fertile coitions of the season, and the time when the last young of the season are capable of independent existence. Hamilton (1939) states that "the season for reproduction is normally considered to be that period when adult animals are concerned with mating and the care of young." The cottontail, as previously shown, normally mates and cares for 3 or 4 litters each year in southern Michigan.

The early March beginning of the breeding season agrees with the observations of Allen (1938b), but is about a month and a half later than was indicated by Trippensee (1936). The season comes to a close in September, and in this respect agrees most closely with the evidence of Trippensee. Although the number of my records is not large, they are scattered evenly throughout the year, so chances for observing the absence or presence of signs of breeding were favorable. The breeding season began suddenly and continued until the last young were weaned about the middle of September. It therefore appears that rabbits in this region have about a six-months' breeding season, starting early in March and extending to early or middle September. Fertile coitions were accordingly made during the period between early March and the middle of August, during which time the testes of males averaged 1.8 inches or more in length.

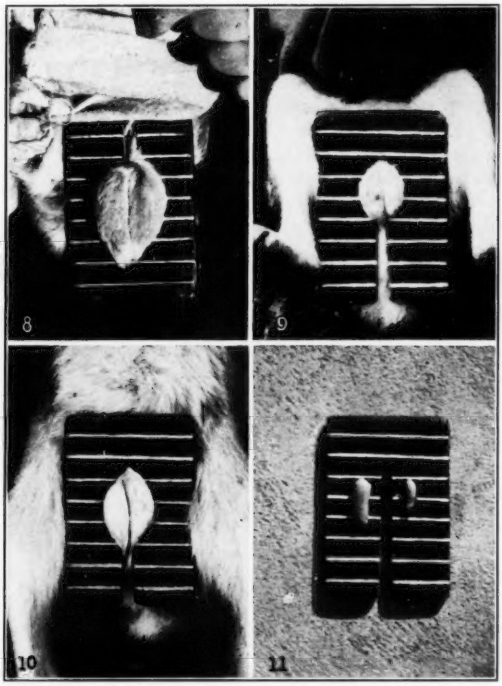


Fig. 8. Size of testes of cottontail on April 23, 1939. Fig. 9. Size of cottontail testes on August 17, 1939. Fig. 10. Size of cottontail testes on December 14, 1939. Fig. 11. The testis on the left is that of an adult; that on the right is from a juvenile. December 14, 1939.

Number of young per litter.—The average size of 12 litters of young observed during 1938 and 1939 was 5.4 (Table 5). A nearly similar average of 5.42 was found by Beule (1940) in Pennsylvania. Allen (1938b) found that evidence from nests and autopsies in Michigan indicated an average litter size of 5.1 young. Trippensee (1936) compiled the data given by several workers in Michigan and calculated that on the basis of 27 litters, the average was 5.04. My data on the average size of litters were secured through autopsies on 5 pregnant females, observations on 4 nests and three litters born in captivity. Differences in average size of litters as determined by these workers and by my study are not significant.

Nesting and care of young.—Only eight cottontail nests were examined during the two years of study. Six of these still contained young when found, but two were empty at the time visited. The young from two others were removed to the experiment station for later study. The two remaining nests, Nos. 1 and 3 of Table 6, were frequently visited to weigh, measure, and photograph the young, some of which were ear-tagged.

Six of the nests examined consisted of a bowl-shaped excavation in the ground; a seventh was shaped similarly, but was formed above ground in a 6-inch bed of straw. The cavity of a nest is sometimes a trifle larger than, and slightly to one side of the top opening. At no time was a nest excavated in the ground in such a way that a tunnel was necessary to reach it. The average size as determined from measurements of four nests is: length of opening, 6.4 inches; width of opening, 4.7 inches; and depth of excavation 3.3 inches. They have been variously lined with rabbit fur, fine grass, and short pieces of grass stems which the rabbit had apparently cut. However, only a faint indication of hair was found lining the nest formed in a bed of straw. Nests containing young were covered with a concealing mat of rabbit hair and grasses. This mat, however, with use, or when tampered with, seems to become partly damaged or destroyed.

TABLE 5.—Records of Cottontail Litters Obtained from Nests, Autopsies, and Births in Captivity.

DATE	NO. OF YOUNG	SIZE	EVIDENCE
3/21	5	24.5 mm.	Embryos
3/23	4	3.5	Embryos
4/9	4	117.5	Born in captivity
4/11	6	....	Nest
4/18	4	105.0	Embryos
4/18	7	22.5	Embryos
4/26	7	....	Nest
5/10 and 11	5	115.0	Born in captivity
5/29	6	112.0	Born in captivity
6/8	5 (?)*	....	Nest
7/25	6	56.0	Embryos
7/31	6	....	Nest

Total young in twelve litters—65.
Average number—5.4.
* A dog had taken 2 of the 5 young before I examined the nest.

TABLE 6.—Location of Cottontail Nests.

NEST NUMBER	LOCATION	COVER	TERRAIN	CLOSEST ESCAPE COVER
A	Grasy field	Weeds	Flat	?
1	Field	Stump	Flat	25 yards
2	Dike bank	Tree	Bank	Immediate
3	Orchard	Bed of straw	Flat	9 yards
4	Field	Stubble	Sloping	?
5	Alfalfa field	Alfalfa	Flat	Immediate
6*	Alfalfa field	Alfalfa	?	Immediate
7	Corn field	Hill of corn	Flat	Immediate

* Not examined by me.

There was no indication that the doe deserted the young in any of three nests in which young were frequently handled. Five days previous to my visit, one nest had been raided by a dog, which took two of the five young. The remaining three were apparently still in good condition when examined. It is doubtful if these young could have survived for five days without their mother's care, as their eyes were not yet open when first disturbed. It was on the fifth day after their eyes opened that the three survivors, which were placed in captivity, were first seen to eat grass. According to Allen (1938b), they were about 16 days of age at this time.

Nest No. 1 was found in a slight concavity against the base of an old stump standing in an open field (Table 6 and Fig. 12). When the nest was disturbed, 6 squealing young scattered in various directions. They were captured, their sex determined, and all but one replaced in the nest. The 4 females and 2 males had their eyes open and were probably about 14-15 days old. The one individual kept captive weighed 74.34 grams, its hind foot measured 38.5 mm. and its ear measured 25 mm. A few hours later that same day, only one male remained in the nest. It was then ear-tagged. Two days later, all five young were again present in the nest at 9:30 A.M., but only 4 remained at 11:30 A.M. (Fig. 14). Tracks in the light snow showed that both an adult rabbit, presumably the mother, and the young had been active about the nest during the previous night. They were absent from the nest on the following day and apparently never returned.

Nest No. 3 was found by a farmer in the corner of an apple orchard. It was in a small 6-inch deep bed of straw, about 9 yards from good cover and a frequently travelled highway. On May 5, six days after discovery, the young were still blind. At this time the total weight of all seven young was 14½ oz., the average length of their ears 16.7 mm., and the hind foot 29.1 mm. The eyes of one rabbit was open on May 7, and of two on May 8. At this time the average ear length was 20.7 mm., and the hind foot 35.7 mm. All six young which were in the nest on May 11 were ear-tagged and weighed (total weight, 18.5 oz.). The seventh individual apparently left the nest one day earlier than the remaining six which were gone on May 12, at which time they were known to be at least thirteen days old.

Sex ratio.—Gerstell (1937a) noted the sex of 6,394 live cottontail rabbits shipped into Pennsylvania from Kansas and Missouri for restocking purposes.

He found that, "of the total in question, 3,246 individuals were females, while 3,148 were males, the respective percentages being 50.8% and 49.2%." Trippensee (1936) examined 226 cottontails, of which ". . . 123 were males, and 93 were females . . .", indicating a ratio of 43 per cent females. Allen (1938b) took 383 rabbits by various methods and found that ". . . 195 were males and 188 were females"; the sex ratio was accordingly 49 per cent females.

Almost all rabbits examined for sex during this study were live-trapped. A few were shot or were picked up dead on the highway. Eight hundred twenty-five rabbits, consisting of 411 females and 414 males, have indicated a sex ratio of 50 per cent females.

A large number of these rabbits were taken on areas closed to hunting during 1939. However, some poaching took place. It is doubtful if the normal sex ratio has been appreciably altered by a higher percentage of males being shot, as might be expected from evidence found by Trautman (Trippensee, 1936) in Ohio, where females were more likely to hole up during cold weather than were males.

Summary on reproduction.—The breeding season of the cottontail has been found to continue from early March to mid-September. This season was determined from a chronological series of measurements on the testes of individual living males, nesting records, autopsies, and by palpating the abdomen of females which were live-trapped.

Individual cottontails in this region frequently have as many as 4 litters in a single season. The average litter size as determined in this study is 5.4. Comparable stages of successive pregnancies were found in 3 females with an average interval of only 29.3 days. Accordingly, cottontails may have fertile coitions within a day or two after parturition.

The sex ratio among 825 rabbits (411 females and 414 males) handled was 50 per cent females.

WEIGHTS OF COTTONTAILS

Weights were taken of all rabbits live-trapped or found dead on the highway in the vicinity of the experiment station during all the seasons of 1938 and 1939. Many were retaken and weighed frequently during the two years of study, others were weighed only once.

Methods of securing and summarizing weights.—The method of weighing rabbits consisted of putting each individual into a small cloth bag, which was then closed by a purse string at the top. The bag was suspended from a spring scale, and the weight of the animal and the bag read. The weight of the bag was then subtracted from the total, and the weight of the rabbit recorded to the nearest half ounce.

Four hundred seventy-seven individual cottontails were weighed a total of 939 times (Table 7). Average weights have been grouped by ten-day periods. If an individual rabbit was weighed more than once during a given ten-day period, its average weight for that period was determined and included

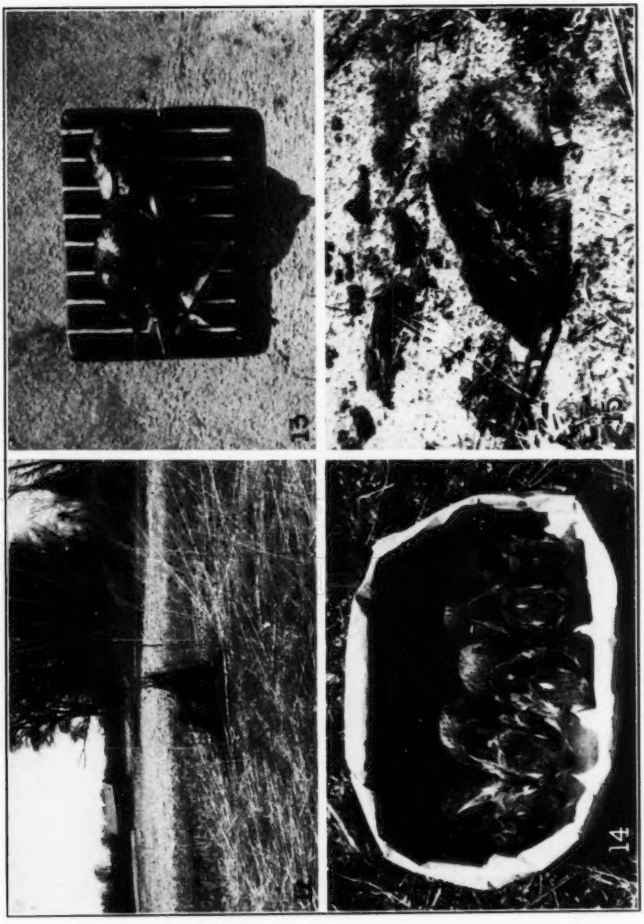


Fig. 12. Nesting site of a cottontail. Nest against base of stump. Fig. 13. A newborn cottontail. Scale: ½ inch between parallel lines. Fig. 14. Young cottontails which will leave nest in a couple of days. April 16, 1939. Fig. 15. Protectively colored juvenile cottontail. Which predator will get him? If he can find the right cover he may live a long time. May 9, 1939.

only as a single datum in calculating the average of the group. The weights of females, males, and juvenile rabbits are given separately. However, it was necessary to combine the data on weights of adults and juveniles after December 10, because some young were as heavy at this time as some known adults. In fact, a few physically mature young may have been unknowingly included in the average weights for adult rabbits during November. The age of most individuals could, however, be ascertained with reasonable certainty until early December. Until this time, the clitori of juvenile females and the testes of juvenile males were usually smaller than the same organs in adult cottontails.

Average weights according to season.—Average weights of cottontail rabbits in this region at the various seasons are: for adult females, 2 lbs. 15.8 ounces during winter, 3 lbs. 3.3 ounces during the breeding season, and 3 lbs. 3.1 ounces during the fall period. Adult males weighed 2 lbs. 13.5 ounces during winter, 2 lbs. 13.2 ounces during the breeding season, and 3 lbs. 2.1 ounces during fall. Average fall weight of juvenile rabbits was 2 lbs. 7.2 ounces for females and 2 lbs. 5.8 ounces for males. Adult females have averaged heavier than males during all periods of the year. This difference in weight between sexes ranged from only 1 ounce during fall to 6.1 ounces during breeding season. Pregnancy was partially responsible for the considerable increase in weight by females during summer. Juvenile females, on an average, were 1.7 ounces heavier than juvenile males during the fall period. According to these figures, females are the larger members of the species at all sasons. The greater weight of females has likewise been noted by Allen (1939), who states that in every group of rabbits sampled, females averaged heavier than the males. This difference in weight varies considerably during the various parts of the year, as will be shown later.

Effects of weather on weights.—Stormy winter weather decreases the weight of cottontail rabbits. Nineteen individual rabbits (8 females and 11 males) which were retaken during more than one of the ten-day periods between January 11 and February 28, show an average decrease of 2.34 ounces in weight. Most of this loss of weight occurred between January 11 and February 10. There were 3.5 inches of snow on the ground on January 18, and a snowstorm accompanied by a stiff northwest wind occurred on January 22. By January 27, 10 inches of loose snow were on the ground. Rabbits were moving very little during this inclement weather. Several cottontails were found occupying burrows, and 2 or 3 were caught while they were sitting in snow-covered forms. This indicated that fresh snow covering the food supply was keeping rabbits under cover. Accordingly, their loss of weight was probably due to lack of proper food. The 8 females lost an average of 3.56 ounces each, while the 11 males lost an average of only 1.46 ounces each. Females lost 3.2 times as much weight as did males. This indicates that males may be less affected by winter weather than are females. However, the data are too inadequate to allow any definite conclusion. A decrease in weight in winter by cottontails was also noted by Allen (1939), who found that a group of rabbits taken in December were 1.7 ounces heavier than another group live-trapped during March. The greater loss of weight in my rabbits is not significant.

The apparent rise in average weight by females between January 20 and January 31, is not significant, because this average is based on only three individuals (Table 7). Two of the females included in the average weight for this period had each lost an average of 4.25 ounces during this period, but the third, a newly taken individual, was large enough to raise the average.

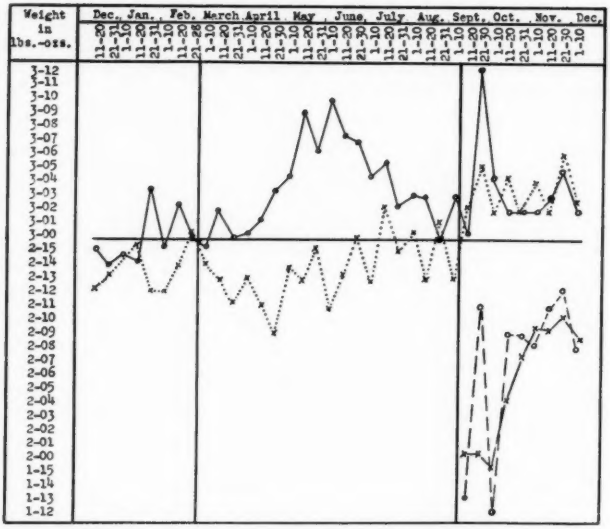
Fluctuations in weight of pregnant females.—Individual females often varied considerably in weight from day to day during pregnancy. As an example, female No. 449 weighed 3 lbs. 8 oz. when she was first trapped on July 11. At that time, she was carrying uterine swellings about the size of a hazelnut. During the ensuing 8 days, she was retrapped daily and gradually lost 4 ounces of weight. When she was taken on July 29th, she weighed 3 lbs. 4 oz. and contained embryonic swellings about the size of a walnut. During the next 6 days, she was retrapped 6 times and regained 4 ounces of weight. This gain in weight occurred at the time during which the embryonic swellings increased from the size of a walnut to a size indicative of embryos approaching full term. In this case, it seems possible that the rabbit may have lost some of its weight because of the constant retrapping, but that the weight of the rapidly growing embryos, the increase in uterine tissues, and the increase in fluids finally compensated for the earlier loss.

The average weight of females gradually increased from 2 lbs. 15.5 ounces in late March to 3 lbs. 9.5 ounces in early June. The average weight gradually decreased during July and August. The increased average weight of females during the breeding season is probably due both to an increase in amount of flesh and their gravid condition.

Except for minor fluctuations, the average weight of adult females changed very little during the fall months.

Seasonal fluctuations in the weight of males.—The weight of adult males does not vary as greatly during the year as does that of females. Average weight of males increased during December and until it reached 2 lbs. 15 oz. in the middle of January. Three and one-half ounces of weight were then lost on the average during the last part of January, because of the inclement weather previously discussed. Males made a slight average gain in weight during the last 20 days of February. At the start of the breeding season (March 1), males were in the best condition (3 lbs.) attained during the winter period. From this time on, however, the average weight of males decreased rapidly until in late April it was only 2 lbs. 8.5 oz. This loss was probably due to an increase in activity during the breeding season. Their average individual range (Haugen, in press) was very large (perhaps 100 acres) at this time of the year. At about the time green vegetation became available (late April) males began to regain some of the weight they lost during the first two months of the breeding season. They continued slowly to gain weight until the middle of September, at which time they averaged 3 lbs. 2 oz. (Graph 2). A sudden rise in average weight (increase to 3 lbs. 5 oz.) during September coincides with the ending of the breeding season.

Increase in weight by juvenile cottontails.—Individual weights of juvenile



Graph 2. Seasonal variations in weights of cottontail rabbits. Key: o———o adult females; ×.....× adult males; o— — o juvenile females; ×———× juvenile males.

rabbits vary widely during the fall period. This is expected because of the large age differences in litters born during the various parts of the breeding season (March to September). Weights of 62 juvenile rabbits taken between September 11 and 20 are dispersed evenly between 11 ounces, and 2 lbs. 13 oz. The amount of deviation from the mean steadily decreases as the fall period progresses. The range of variation of the weights of juvenile rabbits was reduced to 10.5 ounces (2 lbs. 3.5 oz. to 2 lbs. 14 oz.) by the first of December. Average weights of the juveniles are unreliable because of the wide variability of individual weights. However, there is a rapid increase in average weight from September through November (Table 7).

Summary on cottontail weights.—From the evidence presented, it is apparent that weather, season, pregnancy, age and sex have a considerable effect on the weight of the cottontail. Adult females increase considerably in weight during the breeding season, reaching their maximum average weight during early June. The average weight of males, however, decreased considerably during March and April, then slowly increased during the last two-thirds of the breeding season. A further gain in weight by males was noted as the breeding season came to a close. Weights of adult females and males both averaged about 3 lbs. 2.5 oz. during October, November, and early December, but at other seasons, females were always the heavier. A further rise in weight by adult rabbits occurred during the middle of December. Some juvenile rabbits,

however, were as heavy as many adults at this season, and it is therefore necessary to combine weights of all individuals of the same sex after December 11. Inclement weather during January and early February 1939, resulted in an average decrease of 2.34 ounces of weight.

TABLE 7.—Seasonal Weights of Cottontail Rabbits.

		Adult				Juvenile			
		Female		Male		Female		Male	
		Number weighed	Mean weight	Number weighed	Mean weight	Number weighed	Mean weight	Number weighed	Mean weight
Dec.	11-20	8	2-15.0*	16	2-12.0*				
	21-31	5	2-13.5	12	2-13				
Jan.	1-10	5	2-14.5	0					
	11-20	7	2-14	6	2-15				
	21-31	3	2-02.5	4	2-11.5				
Feb.	1-10	6	2-14	13	2-11.5				
	11-20	8	3-02.5	13	2-13.5				
	21-28	4	2-15.5	8	3-00.5				
	Winter	46	2-15.8	72	2-13.5				
March	1-10	10	2-15	18	2-13.5				
	11-20	13	3-01	15	2-12.5				
	21-31	16	2-15.5	18	2-11				
April	1-10	15	3-00	17	2-12.5				
	11-20	25	3-01	21	2-10.5				
	21-30	9	3-03	9	2-08.5				
May	1-10	12	3-04	7	2-13.5				
	11-20	11	3-08.5	14	2-12.5				
	21-31	14	3-06	5	2-15				
June	1-10	5	0-09.5	2	2-10.5				
	11-20	13	3-07	7	2-13				
	21-30	11	3-06.5	7	2-15.5				
July	1-10	11	3-04	2	2-12.5				
	11-20	13	3-05	4	3-02				
	21-31	23	3-02	13	2-14.5				
August	1-10	12	3-02.5	5	3-00				
	11-20	7	3-02.5	3	2-12.5				
	21-31	9	3-15.5	7	3-00.5				
Sept.	1-10	13	3-02.5	10	2-12.5				
	Breeding Season	242	3-03.3	184	2-13.2				
Sept.	11-20	3	3-00	4	3-02	31	1-12.5	32	2-00
	21-30	1	3-12	1	3-05	3	2-10.5	9	2-00
Oct.	1-10	5	3-04	2	3-01.5	4	1-11.5	8	1-15
	11-20	3	3-01.5	2	3-04	12	2-08.5	11	2-05
	21-31	9	3-01.5	10	3-01.5	21	2-08.5	23	2-07
Nov.	1-10	7	3-01.5	3	3-03.5	33	2-08	35	2-09
	11-20	7	3-02.5	4	3-01.5	36	2-10.5	32	2-09
	21-30	2	3-04.5	2	3-05.5	18	2-12	12	2-10
Dec.	1-10	1	3-01	2	3-02	3	2-07.5	4	2-08
	Fall	38	3-03.1	30	3-02.1	161	2-07.5	166	2-05.8

* Weight given in pounds-ounces.

PARASITES OF THE COTTONTAIL RABBIT

Degree of infestation by ectoparasites has been carefully observed on most of the 825 individual cottontails captured during 1938 and 1939. Several of these individual rabbits were reexamined repeatedly during one or more seasons during the two years. At each examination, the degree of infestation by fleas, ticks, and mites was recorded as "light," "moderate," or "heavy." The presence of 5 or 6 individuals of a parasite was called a moderate infestation, while a greater number was considered indicative of heavy infestation. Dead rabbits were sent to the Pathology Laboratory of the Michigan Department of Conservation at East Lansing to be examined for endoparasitic infection.

ECTOPARASITES

Fleas.—Rabbits have usually been infested with a moderate number of fleas during all months of the year. Dr. J. C. Bequaert of Harvard University identified a single specimen as *Cediopsylla simplex* Baker, the common species on cottontail rabbits. The degree of infestation on a single individual cottontail often varied from day to day. This variation is believed to have been in part caused by errors in observing the degree of parasitism. Rabbits which were recorded as free from infestation may have harbored a few hidden fleas. Most of the fleas were usually congregated on the head region of the rabbit.

The only observed ill effect suffered by rabbits from parasitism by fleas was a severe irritation of the hairless inner fold on the anterior edge of the ear. At times during winter, 8 to 10 more fleas occupied this hairless crease. Such extreme cases were usually accompanied by signs of bleeding on the infested area.

Ticks.—Ticks have been found in moderate to small numbers during all months of the year except December, January and February, when they were apparently absent. The only tick found on the cottontail during these 3 winter months was observed on January 17, 1939. Dr. J. C. Bequaert of Harvard University has identified ticks collected from the cottontails as *Haemaphysalis leporis-palustris* (Packard). During March, frequency of infestation by ticks became increasingly greater. A moderate infestation continued until early November, after which their numbers decreased rapidly.

The common point of infestation by ticks was at the base of the ears, and in the short hair about the eyes. Occasionally, they were found in the hairless inner surface of the anterior fold of the ear, as were the fleas. No apparent ill effect from tick infestation has been observed.

Mites.—Mites were found on 6 individual rabbits, and on one litter of young. It is believed, however, that many cases of mite infestation escaped detection. They are so extremely small that they were seen only with a very close examination. In fact, mites escaped detection entirely during 1938. Dr. H. E. Ewing of the U. S. Bureau of Entomology has kindly identified the 3 genera of mites which were found on the cottontails.

Articholaelops glasgowi (Ewing) a mite common on many species of

North American Mammals was abundant on some nestling rabbits found on April 12, 1939. No other records were secured.

Cheyletiella sp., a predaceous mite that feeds on true ectoparasites, was secured from adult cottontails in October, 1939. These mites were found at the base of the head just posterior to and between the ears.

Euhaemagamasus sp., a true parasitic mite, was taken from a cottontail on April 1, 1939. Only a single specimen of this species of mite was collected.

Mange-like condition of skin.—Nine individual rabbits were found with various degrees of flakiness of the skin, but no scab mites were observed. The most extreme mange-like condition was observed on an individual autopsied on April 20, 1939 (Fig. 16). This adult male rabbit was exceedingly emaciated, without hair on the posterior ventral side, and only sparsely furred on the rest of the body. Scrapings were taken from the skin of this animal, and the scaly looking debris examined under a microscope, but no scab mites were found.

Warble fly larvae.—The larvae of two species of warble flies live in cottontails in this area. These species were identified by Dr. Bequaert as *Cuterebra cuniculi* Clark, and *Cuterebra buccata* Fibricius. Parasitism with these pests first became evident during the middle of November. As many as 8 larvae have been observed on a single rabbit at one time. The ventral side of the body is most frequently parasitized, especially the throat and chest region (Fig. 17). Occasionally, larvae were found in the inguinal region (Fig. 18).

One adult fly of *Cuterebra buccata* was incubated from a larva dropped from the scrotum of a rabbit on September 4, 1938. The larva was allowed to burrow into the ground by its own effort (2 inches below surface). On the following day it was transferred into a tin can containing sandy soil. The pupa was buried two inches below the surface of the soil in the can. The can with lid attached, and with top and bottom punched full of nail holes, was then buried flush with the surface of the ground. The nail holes allowed moisture to pass through the can. This improvised incubator was examined for signs of

Fig. 16. Cottontail with a mange-like condition of the skin. April 20, 1939. Fig. 17. Five warble fly larvae on throat of cottontail. Photo by D. L. Allen. Fig. 18. Warble fly larva in scrotum of male cottontail. August 17, 1939.

emergence on several occasions in the early summer of 1939. On July 2, 1939, the fly was found emerged, but dead and partly destroyed by small ants. According to the schedule of examinations of the incubator, this fly emerged on about June 28, 1939. The larva therefore emerged after 297 days of pupation.

Three specimens of *Cuterebra cuniculi* were incubated. On July 26 and 27, 1939, four warble larvae from cottontails were put into two containers and covered with about 2½ inches of damp sand. Both containers were then left in a cool, damp basement room and slightly watered on a few occasions. On September 15, 1939, the first fly was found sitting on the underside of the cheese cloth which enclosed the top of the can. According to schedule of examinations, this specimen emerged after 61 to 63 days of pupation. Two of the remaining three pupae were found emerged on June 8, 1940, 316 or 317 days after leaving the rabbit.. One of the individuals (alive) had apparently emerged on this date, the other was dead and probably emerged a few days earlier. Further records were not kept on the fourth pupa.

ENDOPARASITES

Twenty-one cottontails killed near the experiment station mainly during December, January and February were examined for endoparasites and pathogenic conditions.

The per cent of individual cottontails infected by endoparasites was found to be as follows:

	Individuals parasitized	Per cent of individuals parasitized
Sporozoa *Eimeria* sp.	11	52%
Trematoda *Hasstilesia tricolor*	7	33%
Cestoda *Taenia pisiformis*	10	48%
Cittotaenia pectinata	14	67%
Nematoda *Trichostrongylus* sp.	5	24%

Coccidiosis.—Eleven rabbits (52%) were infected with two species of *Eimeria.* Infections were never found serious in either adult or juvenile wild rabbits, but one juvenile captive cottontail died from a severe case of coccidiosis during the summer of 1939. This juvenile had been held in captivity for 2 months. A necropsy reevaled a distended, necrotic condition of the caecum which was 2 inches long and three-fourths inches in diameter. The entire cavity of the caecum was filled with a "cheesy" looking liquid swarming with coccidia oöcysts.

Yeast.—An extraordinarily heavy concentration of yeast was found in the small intestines of a juvenile cottonwood which died in captivity during the summer of 1939. A case of diarrhea accompanied the condition.

Trematoda.—Hasstilesia tricolor, a fluke, was found in 7 rabbits (33%). Rabbits secured from damp lowland habitats during winter were found to have the most severe infections. The intermediate host of this species probably occurs more frequently in those habitats.

Cestoda.—Larvae of the dog tapeworm, *Taenia pisiformis*, were recovered in 10 cottontails (48%). The number of these cysticerci present in a single cottontail has varied from 1 up to 50. The small bladder larvae were found throughout the body cavity.

The rabbit tapeworm, *Cittotaenia pectinata*, has occurred in 14 of the rabbits (67%) autopsied. In no instance were more than four of these tapeworms present at one time.

Nematoda.—Five cases (24%) of infection with *Trichostrongylus* sp. were found. The degree of parasitism was small in each case.

PAPILLOMAS

Forty cases of papillomas, or "horns," were found among rabbits live-trapped. Affected rabbits were found only between September 1 and December 13, and the abnormality was limited almost entirely to juvenile or sub-adult rabbits. Only 2 of the 40 cases were found on rabbits which were definitely 1 year or more old. The flesh colored swellings most frequently occurred on the feet (Fig. 19), but were also found on the nose, eyelids, lips, ear and back. Rarely, have the swellings reached the size of an inch in diameter.

Tumors evidently disappear from the affected cottontails during winter. Three rabbits which showed tumors in the fall of 1938 were without the gruesome looking warts when recaptured in the summer of 1939.

DISCUSSION OF EFFECTS OF PARASITISM

One case of mortality among cottontails handled during the investigation has been attributed to parasitism. In this case, death resulted from a very severe case of coccidiosis suffered by a juvenile captive rabbit. A second juvenile

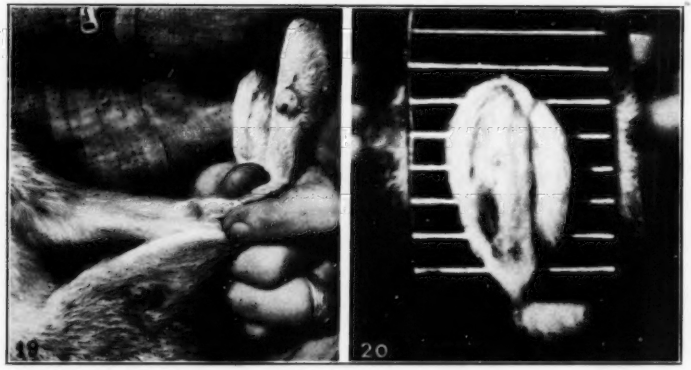


Fig. 19. Papillomas or "horns" on the legs of a cottontail. Photo by D. L. Allen. Fig. 20. Size of cottontail testes on April 1, 1939. Note degenerate left testis. Warble fly larvae parasitized scrotum in 1938. Scale: ½ inch between lines.

rabbit which died unexpectedly in captivity harbored an abnormal concentration of yeast in its intestines and showed signs of diarrhea. It is not known for certain if death resulted from the overabundance of yeast.

A moderate infestation with fleas, ticks, mites, or a moderate infection with trematodes, cestodes and nematodes did not seem to have any apparent influence on the well-being of cottontails. In fact, heavily parasitized rabbits were frequently very fat.

The presence of a mange-like condition in rabbits has not reached a sufficiently large incidence of occurrence to be of any importance. Perhaps some of the 9 cases observed were contracted from the cloth bag which had been used to weigh both rabbits and squirrels. Many of the squirrels which were placed in the bag exhibited severe cases of scab.

Warbles have in three cases caused an abnormal condition of one testis of male rabbits. After the parasitic larva had left its position in the scrotum of the rabbit, it was found that the afflicted testis was very small and degenerate. As far as could be determined, the opposite testis was normal. A year later, it was found that the damaged testis of one rabbit had recovered. The afflicted testis of a second male still remained degenerate the following breeding season (Fig. 20). It seems possible from this evidence that warble fly larvae could in rare instances cause sterility.

The psychic effect on a hunter of the presence of heavy infestations of parasites on rabbits is of importance. Probably, many a rabbit has been discarded because of its unsightly appearance due to the presence of warbles, papillomas, or cysticerci. Warbles ("grubs") disappear from cottontails suddenly in early November.

Accordingly, if the opening of the hunting season on cottontails were delayed until November 15, the waste of meat resulting from the discarding of rabbits with unsightly warbles ("grubs") could be eliminated.

SUMMARY ON PARASITES

Two species of warble fly larvae commonly parasitize the cottontails in this region from July to mid-November. The presence of warble larvae in the scrotum of rabbits caused temporary degeneration of the testis in one rabbit, and permanent degeneration in the testis of a second rabbit.

A flaky, mange-like condition of the skin has been found on nine cottontails during the two years of study.

Fleas and ticks were found in moderate numbers on the cottontails in this region. Fleas were present at all seasons, but ticks were not observed during winter, except on one occasion.

Two species of parasitic and one species of predaceous mites were found during the summer and fall.

The most severe cases of infection with a fluke, *Hasstilesia tricolor*, were found in rabbits taken near bogs and from the lowland.

Two species of tape worms and one of round worms were found in several of the cottontails examined.

The presence of a moderate number of one or more of species of parasites found in the cottontails did not seem to effect the well-being of the individuals to any great extent. In fact, many of the parasitized rabbits were fat.

LONGEVITY

Of 73 adult cottontails (34 females, 41 males) marked during the 1938 breeding season, 21 (6 females, 13 males) were retaken during some part of the 1939 breeding season. These adult rabbits must have been a year or more old when marked in 1938. Accordingly, a minimum of 25 per cent of the 1938 adult population lived to an age of approximately 21 or more months. It is likely that some of the marked rabbits emigrated from the areas studied, and were therefore not retaken. In that event, the per cent of rabbits which reached the age of 21 or more months was larger than indicated. This high per cent (25) of survival to breed 2 or more seasons may be due to the fact that the areas were closed to legal shooting during 1938. However, some poaching did occur. Allen (1939) states, "Of 70 rabbits marked . . . during the first 3 months of 1936, only 12 are known to have lived to the following November." Accordingly, adult cottontails on the areas studied by me were surviving longer than was indicated by Allen's farmland studies. Seven of 29 (24%) cottontails *(Sylvilagus audubonii audubonii)* studied by Ingles (1941) were known to have lived longer than one year.

MORTALITY

PREDATION

New York weasel (Mustela frenata noveboracensis).—Eighteen cottontails were attacked and killed by weasels, which entered through the inch-mesh wire covering on some of the traps. Even traps covered with half-inch hardware cloth did not adequately protect rabbits from weasel attacks. Weasels also entered a few traps through a one and one-fourth-inch hole in the metal door, or made excavations under the wire floor of the trap and attacked the soles of the rabbit's feet. On a few occasions, the flesh was stripped from the toes of the captive rabbit, leaving the bare bones exposed. Such injury probably resulted in ultimate death. One weasel was observed in the act of killing a juvenile rabbit in the wild. Hickie (1940) states that "In making the rounds of its range, the weasel seems to visit each of the holes with which it is familiar." A rabbit cornered by a weasel in a burrow can usually escape (p. 237). Evidence indicates, however, that the weasel is responsible for more cottontail mortality than is any other predator on the area.

Dogs.—During 1938 and 1939 dogs were repeatedly seen in pursuit or possession of cottontails. Two rabbits were definitely known to have been killed by "self-hunting" dogs, and four other dead cottontails were found in the possession of dogs. On three occasions, dogs were found attempting to excavate an animal (probably a rabbit) from a burrow. It was not unusual to find tracks

of dogs in the study areas. A small collie and a large mongrel hound were repeatedly found hunting rabbits on an area three miles in diameter.

Domestic cat.—During 1939, two cottontails were found killed by cats. One of these rabbits contained 4 embryos. Only about 4 individual cats were taken in the live-traps during 1938 and 1939. These were ear-tagged and released in an attempt to determine their range of activity. One adult male cat which had been deserted at a farm which was abandoned was trapped 3.2 miles from its home. It was later discovered back at the abandoned farm home. Two or three other cats on the area have evidently existed in the feral state for 2 or more years. My observations support the statement by Hickie (1940) that stray dogs and cats ". . . take far too large a toll of wildlife while offering nothing in return."

Opossum (Didelphis virginiana).—Only one cottontail was found dead from what appeared to be predation by opossum. The remains of this adult rabbit were found partly pulled into the base of a standing hollow tree. Only a portion of the hind quarters were eaten. Blood stained spots on the inside of the skin of the head and neck region indicated that the rabbit was bitten while still alive.

Red fox (Vulpes fulva).—Information on the interrelationship of fox and cottontail in the areas studied is lacking. Tracks of foxes were found on a few occasions during 1938 and 1939.

Coyote (Canis latrans).—At least one coyote was present in the region during 1939. No signs of predation were found.

Badger (Taxidea taxus).—A badger den was located on one of the management areas, and trails of this species were frequently observed, but at no time was evidence found which indicated predation on rabbits by badgers.

Raccoon (Procyon lotor).—Raccoon are common on the areas. No signs of predation on cottontails were found.

Hawks.—Broad-wing *(Buteo platypterus)*, red-tail *(Buteo borealis)*, and marsh hawks *(Circus hudsonius)* prey on the cottontail in this area. One nest of each species was located. In each case, there was an apparent scarcity of rabbits in the immediate vicinity of the nest. Fur of juvenile cottontails was abundant about the broad-wing hawk's nest. Size of the hind feet of all rabbit remains taken from the marsh hawk nest indicated that nothing larger than an immature rabbit was eaten. Red-tail hawks have been found feeding on the remains of adult cottontails. Hickie (1940) states that the "big hawks" lose importance because ". . . mostly young, instead of adult rabbits appear in their diet. . . ." It should be remembered, however, that a dead young rabbit can never become a live adult.

Owls.—Fresh cottontail remains were found on several occasions in the nests of both Barred *(Strix varia)* and Great Horned *(Bubo virginianus)* owls. Juvenile as well as adult rabbits were represented. Owls were found nesting only in the large timber on the lowland. The greatest predation pressure by these two species was probably exerted on the cottontails occupying the lowland.

Crow (Corvus b. brachyrhynchos).—One freshly-killed juvenile rabbit was taken from a crow. The hind foot of the rabbit was 40 mm. in length, which indicates that it had either been taken from, or had only recently left, the nest.

Black Snake (Elaphe obsoleta obsoleta).—Two juvenile cottontails were recovered from a 5½-foot black snake collected on the area by R. D. Montgomery. One of the young taken from the stomach of the snake weighed 78 grams and its hind foot measured 42 mm. The size of this rabbit indicates that it was about 15-16 days old, at about which age cottontails leave the nest.

MORTALITY FROM EXPOSURE IN TRAPS

Only 7 rabbits died during the study from exposure in traps. Six of these rabbits were overcome by heat, and one died in a trap during severe winter weather. A rabbit can evidently not endure direct exposure to hot summer sunlight for more than a few hours. As a precautionary measure during summer, traps were placed in shade whenever possible. No rabbit should be allowed to remain in a trap exposed to direct summer sunshine later than 9 A.M. The single mortality from exposure in a trap during cold weather occurred on a night with a fresh snowfall and a minimum temperature of 10 degrees Fahrenheit.

HIGHWAY MORTALITY

During 1938 and 1939, 31 cottontails were found dead on Highway M89, and the side roads between Allegan and the experiment station. This number included 12 females, 13 males, and 6 of unknown sex. None of the females examined was pregnant.

During the latter years, numerous papers have appeared listing the numbers of rabbits killed by highway traffic. I do not believe the effect of such mortality is as serious as is often suggested. Automobiles merely kill the rabbits and leave the resulting carrion for other species to devour. Predators which are attracted to the highways by the carrion will have less necessity to kill their own prey. Undoubtedly, a few predators so attracted will themselves become traffic victims.

INJURIES

Seventy-six individual rabbits from a total of 2,113 captures (includes recaptures) have injured themselves while captive in traps. These injuries were as follows: skinned forehead and nose, 68; broken toes, 7; broken leg, 1; and one struck across the neck by the falling trap door.

The skin of ten individual rabbits was torn while handling. The skin of juvenile rabbits is very susceptible to tearing. However, tears in the skin were frequently mended by bringing the torn edges back together and then matting chewing gum into the fur along the tear. The young have often survived severe tears in the skin.

None of the rabbits trapped has shown signs of serious injury received in nature. However, their ears and back frequently showed scars which were evidently signs of combat.

PREDATION ON COTTONTAILS IN BURROWS

Usually, when a shortage of rabbits becomes apparent, the public casts the blame on predation. Often it is claimed that opossums, weasels and skunks raid burrows and eat the cornered rabbits. Seton (1929) tells of the destruction by skunks and weasels of rabbits in burrows.

EXPERIMENTAL EVIDENCE ON PREDATION IN BURROWS

Ten individual experiments on predation by skunks, opossums, and weasels on rabbits occupying burrows were performed. Facilities for the experiment consisted of a specially constructed burrow with an attached lightproof observation pit, and a two-compartment pen above ground. A drop door regulated by a string was used to control the movement of the predator from one compartment of the pen to the other. One end of the pen was connected to a wire-lined burrow (about 6″ diameter) which led downward at a grade of about 25 degrees. At a point 6 feet from the pen and 3 feet below the surface of the ground, the burrow reached the side of the observation pit, turned, and continued parallel along two sides of the pit. A piece of glass from an old car windshield was used to form the side of the burrow which was open to view from the observation pit. The burrow had only one exit. The pit was provided with a light-proof lid so that the observer could sit unseen as he watched the animals with a flashlight covered with red cellophane. On a few occasions, the animals assumed a cautious attitude towards the light; at other times, they ignored it.

Experiments with a skunk (Mephitis mephitis nigra).—Four separate trials were made to see if a hungry skunk would kill a rabbit confined in the experimental burrow. An adult skunk which had been in captivity for about 3 months, and wild adult cottontails were used in the experiments. The skunk, which had been starved for 4 or 5 days prior to the experiment, was introduced into the burrow which contained an adult rabbit. From the observation pit, it was observed that the skunk pursued the rabbit downward. At the end of the burrow, the rabbit quickly turned and met the skunk head on. It quickly forced its way past the skunk and dashed out of the burrow. The skunk remained with a mouthful of rabbit hair. Two additional experiments gave similar results. On a fourth trial, the rabbit stayed at the end of the burrow facing the skunk, but seemed to be sitting or lying on its rump, kicking viciously with both hind feet. The skunk was thus effectively warded off. Shortly after the light was flashed on, the skunk backed away about a foot and remained motionless. The animals were left in this position. Next day the rabbit was found sitting in the pen; the skunk was asleep in the hole.

Experiment with an opossum.—An adult wild opossum which had been starved for 10 days was introduced into the predation burrow containing a rabbit. The rabbit retreated to the end of the burrow as the opossum approached downward. The opossum had to be prodded downward into the hole. As it came close to the rabbit, it seemed to bare its teeth in a defensive snarl and shrank back slightly at each movement of the rabbit, which seemed unalarmed. After about half an hour of observation with no action, the animals

were left to themselves. On the following day, the opossum was found curled up asleep in his pen above ground.. The partly eaten rabbit lay at his side. It is possible that the rabbit escaped from the burrow and into the pen before it was killed, as there was no fresh blood in the burrow.

Experiments with a New York weasel.—Four different weasels were used in five experiments on predation of rabbits in the experimental burrow. Each of these weasels was live-trapped and was denied food on the day of the experiment.

An adult male weasel was allowed to enter the experimental burrow which contained an adult female cottontail. At the time the weasel entered, the rabbit sat facing outward at a point 3 feet from the end of the burrow. The weasel came directly to the rabbit, which remained motionless. As the weasel's nose touched the fur of the rabbit, it seemed to hesitate momentarily, then charged the rabbit, trying to secure a hold at the base of the skull. The rabbit quickly backed down the burrow a foot or two, then dashed forward, forced its way past the weasel, and ran from the burrow. The weasel gave up pursuit at the mouth of the burrow. Apparently, the rabbit was unharmed.

During an additional experiment with other individuals, the rabbit sat facing downward in the burrow when the weasel made his initial attack, attempting to secure a hold at the nape of the neck. This rabbit ran to the end of the burrow where it sat with its nose in the far corner. As the weasel rushed in to secure a hold on the neck, the rabbit quickly turned by rotating its head to a direction away from the weasel, and escaped unharmed from the burrow.

In only one of five experiments did a weasel follow the rabbit into the pen and continue the attack. This weasel succeeded in killing the rabbit after about 2 minutes of intermittent attack. Its killing technique consisted of striking the rabbit at the base of the neck, inflicting one or two bites, and then retreating. After about one and one-half minutes of repeated attacks, the rabbit became increasingly weak. As soon as the rabbit became too weak to dash wildly about the pen, the weasel struck again and hung on, biting viciously at the base of the skull until the rabbit was dead. During one of the early attacks, the rabbit was successful in dealing the weasel a severe blow by means of its hind legs, but this blow did not discourage the weasel. The chief aim of the rabbit seemed to be to find some avenue of escape.

In each of the five experiments with weasels and rabbits, the rabbit emerged unharmed from the burrow.

DISCUSSION OF PREDATION IN EXPERIMENTAL BURROW

Experiments on the vulnerability of cottontails occupying an artificial burrow have shown that their defense from the attacker has consisted mainly in flight. In this situation, however, the only means of flight for the rabbit was to charge the enemy head on and force its way past. This the rabbits did successively in 9 of the ten experiments. On the tenth experiment a cottontail successfully warded off a skunk by sitting at the end of the burrow and thrash-

ing the skunk with its powerful hind legs. Seton (1929) relates how one Rev. Griggs H. Thompson, in Missouri, observed a cottontail leaping over the body of a skunk, striking it with its hind feet. He says the skunk had been dead only a few minutes. In defense of their young, cottontails have been found to similarly attack a cat (Ingersoll, 1907) and a snake (Kennicott, 1857). Although rabbits may sometimes be killed in burrows in the wild, the evidence from my experiments indicates that rabbits are often able to escape or to defend themselves against attack.

SUMMARY ON MORTALITY OF COTTONTAILS

Weasels, stray dogs, and feral cats, in the order listed, are important enemies of cottontails in the area. Only one case of rabbit mortality has been attributed to the opossum. Such predators as fox, badger, coyote and raccoon occurred on the area, but no evidence was found to indicate theiir relationship to the cottontail.

The avian foes of the rabbit consist of hawks (Red-tail, Marsh, and Broad-wing), owls (Great Horned and Barred), and crows.

No rabbits have died in live-traps from injury suffered while struggling to escape, but 6 individuals succumbed from exposure to summer sunlight, and 1 from exposure to severe winter weather.

Experiments on the vulnerability of cottontails which occupy burrows has shown that they are capable of escaping from opossums, skunks, and weasels which attempt to prey on them in burrows.

The most serious predation in the region resulted from the activity of hawks and weasels.

INDIVIDUAL RANGE OF COTTONTAILS

Home range requirements of adult female cottontails on sandy upland areas were 22.5 acres during the breeding-season; during fall, slightly over 15 acres; and during winter, 14 acres (Haugen, in press). Adult males roamed over an area probably 100 acres or more. During late summer, juvenile rabbits occupied an average of 9.3 acres. This area increased with the development of the young until fall at which time the juvenile females occupied 14.6 acres and the males 13.5 acres.

In southwestern Michigan, breeding female cottontails occupied home ranges which were rarely trespassed upon by other breeding females (Haugen, in press). Adult males, however, seemed to roam over large areas in search of mates, which they apparently soon forsook to search for others. Home ranges of males accordingly overlapped indiscriminately.

Cottontail populations.—On an average, the breeding population of cottontails on the sandy upland (1938 and 1939) consisted of about one rabbit per 17 acres (Haugen, unpublished manuscript). During fall, the population increased to one rabbit per 10 acres. The extremes in cottontail populations on the six 160-acre study areas consisted of a minimum of one rabbit per 32 acres during spring, and a maximum of one rabbit per 7 acres during fall.

EFFECT OF COVER ON POPULATION DENSITY

A relationship has been found to exist between the density of the cottontail population and the type of cover available. This relationship has been demonstrated by live-trapping rabbits at stations spaced at 110-yard intervals in a pattern, with a relationship similar as have the center points of each of 49 contiguous squares on a checkerboard. Each square represents an area of 2.5 acres with a trap station at its center (Haugen, in press). The cover on such a trap square, extending half the distance to the nearest surrounding trap stations, will statistically have the greatest influence on the number of rabbits captured at the given station. It is recognized, however, that the number of rabbits caught at any trap station will be influenced in part by the cover on adjacent trap squares. By comparing the catch of cottontails at various trap stations, with the cover densities of the respective trap squares, it is possible to evaluate the influence of cover on the population of rabbits.

The densities of the forest canopy on 293 trap squares on the management areas have been classified as follows: below 12.5 per cent, 25, 50, 75, and above 87.5 per cent dense (Table 8). As an example, I have considered that a canopy which is 50 per cent dense will on the average shut out from 37.5 to 62.5 per cent of the sunlight. The classification was made from the appearance of the cover on an aerial photograph, aided by my knowledge of the area.

Effect of cover on catch during breeding season and fall.—Trapping results during the breeding season and fall show that in trap plots with less than 12.5 per cent of forest canopy, a catch equal to 4.65 per cent of the trap nights (one trap set one night called a trap night) was secured; under a 25 per cent canopy, there was a 3.86 per cent catch; under a 50 per cent canopy, 3.46 per cent catch; under a 75 per cent canopy, 2.38 per cent catch; and under a canopy

TABLE 8.—Relationship of the Density of the Forest Canopy to the Catch of Rabbits During the Breeding Season, Fall and Winter.

Completeness of forest canopy	Number trap squares	Number rabbits	Number trap nights	Per cent trap nights filled
During breeding season and fall:				
below 12.5%	32	208*	4,473	4.65
25.	47	241	6,251	3.86
50.	57	252	7,292	3.46
75.	64	186	7,802	2.38
above 87.5%	93	263	11,304	2.32
During winter:				
below 12.5%	32	3	384	0.78
25.	47	8	459	1.74
50.	57	4	362	1.10
75.	64	18	752	2.39
above 87.5%	93	53	1,469	3.63

* Sum of all rabbits taken on given trap squares. Each individual rabbit counted once for each trapping period in which it was captured on the trap square.

denser than 87.5 per cent a catch equal to only 2.32 per cent of the trap nights was taken (Table 8). It is evident that as the density of the forest canopy increased, the per cent of catch per trap night decreased. In other words, the size of the catch varied inversely with the density of the forest canopy.

Roughly, the number or density of shrubs varied on the trap squares inversely with the density of the forest canopy. The abundance of shrubs is dependent upon the amount of sunshine which reaches the ground. Trapping records, accordingly, show that the population density of rabbits on an average varies directly with the amount of shrubs present. This information can be used in managing an area for cottontails. Thus, by opening the forest canopy to encourage growth of shrubs, it can be expected that an increase in the population of cottontails will result. In support of this evidence, Morton and Sedam (1938) in Pennsylvania have found that cottontail populations increased in areas where release cutting was practiced. Allen (1939) states that "One of the natural coverts on the Kellogg Farm that appeared to be most favored by rabbits in fall and winter was a cut-over oak and hickory brush area . . . the 5-acre plot contained a large number of old skunk and woodchuck burrows that were intensively used by the rabbits." As a contrast, it has been shown in Pennsylvania that where the food and cover of the varying hare was destroyed by deer, the number of hares decreased greatly (Luttringer and Gerstell, 1939).

Effect of cover on catch of cottontails during winter.—During winter, a catch equal to 0.78 per cent of the trap night was secured in areas which in summer had a forest canopy less than 12.5 per cent dense; areas with a 25 per cent canopy yielded a 1.74 per cent catch; 50 per cent canopy, 1.10 per cent catch; 75 per cent canopy, 2.39 per cent catch; and under canopies which were denser than 87.5 per cent, the catch was equal to 3.63 per cent of the trap nights. Accordingly, the catch of rabbits during winter was highest in areas with the denser stand of trees (dense canopy during summer), a condition which is the reverse of that found during spring, summer and fall seasons (Table 8). The figures for winter catch, however, are small and probably undependable, because they are based only on trapping records from the Artificial Burrow, Brush-pile, Check, and Removal Areas. During the winter, rabbits migrated from two of the study areas even from the denser stands of large crowned trees which here appear to be most frequently occupied at this season. In two other areas (one provided with an abundance of artificial burrows, the other provided with an abundance of brush piles), the rabbits avoided the more open places and made considerable use of the artificial cover in the denser stands of trees, but only where a sufficient amount of food was available.

Summary of effect of cover on catch of cottontails. — During spring, summer and fall, cottontails preferred to occupy areas which had a minimum of large crowned trees, but in which generous amounts of shrubby vegetation occurred. In winter, however, they migrated to the lowland unless additional cover such as artificial holes and brush piles were provided. Where such cover was provided, the rabbits used it during winter most frequently among the denser stands of trees, but only where a sufficient amount of food was available.

DISCUSSION

At the rate of reproduction found during this investigation, adult female cottontails may bear as many as 22 young per season (four litters at 5.4 young per litter). Accordingly, factors other than reproductive rate are limiting cottontail populations on the areas.

Competition for home sites or territories by adult females may at times serve to limit populations, but did not do so here because there seemed to be an excess of suitable home sites available. It is recognized that rabbits which occupied the least favorable sites probably suffered greatest mortality by predation.

Intensive study of a 160-acre area revealed that only about one out of every five young survived until fall (Haugen, unpublished manuscript). It is not known that disease or parasites caused any appreciable loss on the areas studied.

Predator pressure is evidently exerted throughout the year, but no continued precise measure of it was secured. The population of predators on the areas appeared to be only average.

In general, there was a deficiency in prey species on the sandy upland areas. This deficiency, coupled with inadequacy of escape cover, makes the cottontail on these areas particularly vulnerable to predation.

Summary

A two-year intensive field study on the cottontail rabbit at the Swan Creek Wildlife Experiment Station at Allegan, Michigan, has shown the following:

The winter food of the cottontails on the upland areas consists mainly of the bark and twigs of white oak, flowering dogwood, sassafras, black oak, and New Jersey tea in the order listed.

As many as four litters in a single season are reared in this region by a single female, and the females apparently breed immediately after parturition. The average number of young per litter during the period of study was 5.4.

Weights of cottontails have varied according to sex, pregnancy, age, season, and weather. The average weight during the hunting season is 3 lbs. 3 oz. for the females, 3 lbs. 2 oz. for the males, and about 2.5 lbs. for the immature.

The most important enemies of the cottontail in the region are weasels, stray dogs, feral cats, and hawks (red-tail, broad-wing, and marsh). Experiments on the vulnerability of cottontails in an artificial burrow have shown that they are capable of escaping or defending themselves in such quarters.

An ecologic relationship between the population density of cottontails and the density of the prevailing ground cover of shrubs has been demonstrated; namely, that rabbits most frequently occupy areas with a generous amount of low ground cover, and may completely avoid locations with a dense forest canopy and no ground cover.

Appendix

CHECK-LIST OF PLANTS

The species of plants listed here are found on the sandy upland areas of the Swan Creek Wildlife Experiment Station, Heath and Valley townships, Allegan County, Michigan. Almost all species were collected on the cottontail rabbit study areas. Except where otherwise stated,the identifications were made by Betty M. Robertson of the Department of Botany, University of Michigan. Source of nomenclature is that of Deam's "Flora of Indiana" (1940).

Herbs:

Ambrosia elatior L. (Common Ragweed)
Andropogon furcatus Muhl. (Big Bluestem)
Anemone virginiana L. (Tall Anemone)
Antennaria plantaginifolia L. (Plaintainleaf Pussytoes)
Apocynum androsaemifolium L. (Spreading Dogbane)
Aquilegia canadensis L. (American Columbine)
Arabis lyrata L. (Lyreleaf Rockcress)
Arenaria stricta Michx. (Rock Sandwort)
Aronia arbutifolia (L.) Ell. (Chokeberry)
Artemisia caudata Michx. (Wormwood)
Asclepias amplexicaulis J. E. Smith (Milkweed)
Asclepias tuberosa L. (Butterflyweed)
Asparagus officinalis (Tourn.) L. (Garden Asparagus)
Aster azureus Lindl. (Azure Aster)
Aster Drummondii Lindl. (Drummond Aster)
Aster laevis L. (Smooth Aster)
Aureolaria virginica (L.) Farw. (Downy False Foxglove)
Brassica kaber var. *pinnatifida* (Stokes) Wheeler (Charlock)
Caltha palustris L. (Marsh Marigold)*
Campanula rotundifloia var. *intercedens* (Witasek) Farw. (Harebell)
Cardamine bulbosa (Schreb.) BSP. (Bulb Bittercress)*
Carex pennsylvanica Lam. (Sedge)
Claytonia virginica L. (Virginia Spring Beauty)
Comandra Richardsiana Fern. (Richards Bastard Toadflax)
Coreopsis lanceolata L. (Lance Coreopsis)
Coreopsis lanceolata var. *villosa* Michx.
Cyperus filiculmis Vahl.
Desmodium viridiflorum (L.) Beck (Velvet-leaf Tickclover)
Epigaea repens L. (Trailing-arbutus)
Eragrostis spectabilis (Pursh) Steud. (Purple Lovegrass)
Erigeron pulchellus Michx. (Robin's Plantain)
Erigeron ramosus (Walt.) BSP. (Narrowleaf Whitetop)
Erodium cicutarium (L.) L'Her. (Storksbill)
Euphorbia corollata L. (Flowering Spurge)
Euphorbia Cyparissias L. (Cypress Spurge)
Fagopyrum esculentum Moench. (Buckwheat)
Fragaria virginiana Duchesne (Virginia Strawberry)
Gaultheria procumbens L. (Wintergreen)
Geranium maculatum L. (Wild Geranium)
Gnaphalium obtusifolium L. (Old-field Balsam)
Helianthemum canadense (L.) Michx. (Rockrose)
Helianthus divaricatus L. (Sunflower)
Helianthus occidentalis Riddell. (Sunflower)
Hepatica americana (DC.) Ker. (Roundlobe Hepatica)
Hypericum perforatum L. (Common St. Johnswort)
Koeleria cristata (L.) Pers. (Junegrass)
Krigia virginica (L.) Willd. (Dwarf Dandelion)
Lepidium virginicum L. (Peppergrass)
Lespedeza virginica (L.) Britt (Slender Bushclover)
Liatris cylindracea Michx. (Gayfeather)
Liatris scariosa (L.) Willd. (Gayfeather)
Linaria canadensis L. Dumort. (Toadflax)
Lithospermum canescens (Michx.) Lehm. (Puccoon)
Lupinus perennis L. (Sun-dial Lupine)
Lycium halimifolium Mill. (Common Matrimony-vine)
Lysimachia lanceolata Walt.
Oenotheria pycnocarpa Atkinson & Bartlett. (Evening-primrose)
Oenotheria cymatilis Bartlett.
Opuntia humifusa Raf. (Prickly Pear)
Osmunda cinnamomea L. (Cinnamon Fern)
Panicum depauperatum Muhl. (Panicum)

Panicum pseudopubescens Nash. (Panicum)
Pedicularis canadensis L. (Early Woodbetony)
Penstemon hirsutus (L.) Willd. (Eastern Penstemon)
Poa pratensis L. (Kentucky Bluegrass)
Polygala polygama Walt.
Polygonatum canaliculatum (Muhl.) Pursh. (Solomon's Seal)
Polystichum acrostichoides (Michx.) Schott (Christmas Fern)
Potentilla recta L. (Cinquefoil)
Potentilla simplex Michx. var. *typica* Fern (Cinquefoil)
Prunella vulgaris var. *lanceolata* (Bart.) Fern. (American Shelfheal)
Pyrola elliptica Nutt. (Shinleaf)*
Ranunculus fascicularis Muhl. (Tufted Buttercup)
Ranunculus hispidus Michx. (Bristly Buttercup)*
Saponaria officinalis L. (Bouncing-bet)
Selaginella rupestris (L.) Spring. (Rock Selaginella)
Senecio aureus L. (Golden Groundsel)
Smilacina racemosa (L.) Desf. (False Solomon's-Seal)
Solidago caesia L. (Wreath Goldenrod)
Solidago canadensis L. (Canada Goldenrod)
Solidago nemoralis Ait. (Old-field Goldenrod)
Stipa avenacea L. (Blackseed Needlegrass)
Stipa spartea Trin. (Porcupine Grass)
Tephrosia virginiana (L.) Pers. (Smooth-leaflet Virginia Goatrue)
Tradescantia canaliculata Raf. (Glaucous Spiderwort)
Tragopogon pratensis L. (Goatsbeard)
Trillium grandiflorum (Michx.) Salisb. (Large flower Trillium)
Verbascum Thapsus L. (Mullein)
Verbena canadensis (L.) Britt. (Rose Verbena)
Vicia Cracca L. (Vetch)
Vicia villosa Roth. (Hairy Vetch)
Viola conspersa Reichenb. (Dog Violet)*
Viola sagittata var. *ovata* (Nutt.) T. & G.
Viola vallens (Banks) Brainerd (Smooth White Violet)*
Viola pedata L. (Birdfoot Violet)
Viola sororia Willd. (Downy Blue Violet)
Vitis palmata Vahl. (Catbird Grape)

Shrubs:
Alnus incana (L.) Moench var. *americana* Regal. (Speckled Alder)*
Amelanchier canadensis (L.) Medic. (Downy Shadblow)
Amelanchier humilis Wieg. (Low Shadblow)
Ceanothus americanus L. (New Jersey Tea)
Chamaedaphne calyculata (L.) Moench. (Leatherleaf)*
Cornus florida L. (Flowering Dogwood)
Cornus racemosa Lam. (Gray Dogwood)
Crataegus sp. (Hawthorn)
Gaylussacia baccata (Wang.) K. Koch. (Black Huckleberry)
Rhus typhina L. (Staghorn Sumac)
Ribes americanum Mill. (American Black Currant)
Rosa palustris Marsh. (Swamp Rose)
Rosa carolina L. (Pasture Rose)
Rubus allegheniensis Porter (Allegheny Blackberry)
Rubus flagellaris Willd. (Northern Dewberry)
Salix humilis Marsh. (Prairie Willow)
Salix sp. (Willow)*
Vaccinium corymbosum L. (Highbush Blueberry)*
Vaccinium angustifolium Ait. (Lowbush Blueberry)
Vaccinium vacillans Kalm ex Torrey. (Dryland Blueberry)
Viburnum acerifolium L. (Mapleleaf Viburnum)

Trees:
Acer rubrum L. (Red Maple)
Carya ovalis (Wang.) Sarg. (Small-fruited Hickory).
Malus coronaria (L.) Mill. (Wild Sweet Crab)
Malus pumila L. (Common Apple)
Ostrya virginiana (Mill.) K. Koch. (Hop-hornbeam)
Pinus resinosa Ait. (Norway Pine)
Pinus Strobus L. (Northern White Pine)
Populus alba L. (White Poplar)
Prunus serotina Ehrh. (Black Cherry)
Prunus virginiana L. (Common Chokecherry)
Quercus alba L. (White Oak)**
Quercus velutina Lam. (Black Oak)
Sassafras albidum (Nutt.) Nees. (Sassafras)

* Taken at the edge of a leather leaf bog.
** Identification by the writer.

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A Study of the Cave Bats of Minnesota with Especial Reference to the Large Brown Bat, Eptesicus fuscus fuscus (Beauvois)[1]

G. N. Rysgaard

Introduction

Bats have figured in the legends and arts of nearly all cultures from time immemorial, and usually they have been portrayed as omens of evil. Through the ages but comparatively little has been learned of their habits and ways. Even today numerous superstitions enshroud these mystical creatures. Because of the scantiness of knowledge concerning the bats of Minnesota, this study was seriously undertaken in the fall of 1940; although many notes had been gathered previously.

In Minnesota there are found seven species of bats which fall into two convenient arbitrary groups—those known as tree bats which roost in trees and on cliff faces and those termed cave bats which gather in caves, buildings, and hollow trees. The tree bat species are normally present during the summer months only, leaving the state each fall to migrate far southward. The cave bats, on the other hand, remain in greater or lesser numbers throughout the winter season at which time they resort to caves and buildings for shelter. This study concerns itself solely with those species of cave bats found within the state borders of Minnesota. The following species are known to occur in the state:

a. *Myotis l. lucifugus* (LeConte), Little Brown Bat.
b. *Myotis keenii septentrionalis* (Trouessart), Big-eared Little Brown Bat.
c. *Pipistrellus subflavus obscurus* Miller, Dusky Georgian Bat.
d. *Eptesicus fuscus fuscus* (Beauvois), Large Brown Bat.

Bats have received little attention from the mammalogists of this state during years past. The first published report containing notes on the bats of Minnesota is that of A. E. Ames (1873), which list included *Vespertilio lucifugus* LeConte (=*Myotis lucifugus*) and *Nycticejus crepuscularis* Allen (= *Nycticeius humeralis*). The latter mentioned species has never since been reported for the state and undoubtedly was a misidentification of *Eptesicus fuscus*.

C. L. Herrick (1885) listed only *Myotis lucifugus* for the Big Stone Lake region; in his state list (1892), he included both *Myotis lucifugus* and *Eptesicus fuscus* and gave no credence to Ames' record of *Nycticeius humeralis*.

[1] A thesis submitted to the Graduate School of Michigan State College of Agriculture and Applied Sciences in partial fulfillment of the degree of Master of Science, August, 1941.

C. E. Johnson (1916) added *Myotis keenii septentrionalis* to the state list. *Pipistrellus subflavus* was first recorded by G. A. Swanson and C. Evans (1936).

Caves of Minnesota

The caves of Minnesota are of two types, namely: the natural limestone caves of the southern portion of Minnesota and the sandstone caves which have been man made for purposes of storage, raising mushrooms, mellowing brewery products, and quarrying sandstone for abrasive material.

The natural caves of the state are primarily of the "sink hole" type. Before the glacial period immense valleys of erosion were excavated in the areas of the Galena and Trenton Limestone, producing deep, narrow, perpendicular gorges. In such narrow gorges, neither the drift nor the loess-loam was deposited in such compactness as to entirely close up the pre-existing water courses. Partially closed as they were, the erosion action of the subterranean waters carried on a process of re-excavation, resulting in periodic collapsing of the surface soil to produce a "sink hole." The openings so produced granted an entrance to the caverns. Situated below the frost line and kept humid by the infiltration of surface water, these caves offered ideal winter quarters for bats.

The sandstone caves, being smaller in size and more exposed, were generally cooler and less humid. In the more extensive caves of this type, seepage chambers existed in the innermost ramifications offering conditions similar to those found in the natural caves. The type of cave and the conditions existing therein have a strong bearing upon the winter populations as shown in Table 1.

Method of Study

This study was planned on the basis of a long time program, and it was realized at the onset that if much of the desired information was to be obtained, it would be necessary to mark a large number of individuals for future identification.

Many methods of tagging have been employed in the past to mark bats. Eisentraut (1934) placed aluminum bands about the humerus, Mohr (1934) employed fingerling tags which were attached to the ears, and attempts have been made to tattoo the wing membranes. It was decided that the most satisfactory method was to place No. 1 aluminum bird bands about the tibia. These bands are issued by the Fish and Wildlife Service of the U. S. Department of Interior and bear a serial number on the outside and a return legend, "Notify Biol. Surv. Wash. D. C.," on the inside. These bands seldom seemed to cause injury when closed tightly against the interfemoral membrane, and they in no way inhibited flight.

During the winter season of 1940-41, all known caves in Minnesota were visited and examined for bats. Capturing bats in wintering caves is comparatively simple, as most of them are found in a dormant state and may be easily plucked from the walls. Those which have secreted themselves in the crevices are quickly extracted with long forceps. More than 600 bats have been banded during the past year.

TABLE 1.—Minnesota caves and relative abundance of species inhabiting each.

ARTIFICIAL SANDSTONE CAVES

Location	Temp.	Rel.Hum.	Species	No.
Jordan, Minn.	41.0° F.	....	*Eptesicus f. fuscus*	8
Feb. 2, 1941	48.0° F.	99%	*Pipistrellus subflavus obscurus*	6
St. Peter, Minn.	48.0° F.	99%	*Pipistrellus subflavus obscurus*	1
Oct. 24, 1940	42.0° F.	86%	*Eptesicus fuscus fuscus*	1
	48.0° F.	99%	*Myotis l. lucifugus*	2
	48.0° F.	99%	*Myotis keenii septentrionalis*	3
St. Peter, Minn.	48.0° F.	99%	*Pipistrellus subflavus obscurus*	1
Dec. 21, 1940	48.0° F.	99%	*Myotis keenii septentrionalis*	1
	40.0° F.	85%	*Eptesicus f. fuscus*	250
Stillwater, Minn.	35.0° F.	91%	*Eptesicus f. fuscus*	200
Dec. 22, 1940				
Red Wing, Minn.	45.0° F.	99%	*Pipistrellus subflavus obscurus*	2
Jan. 3, 1941	35.0° F.	75%	*Eptesicus f. fuscus*	400
	43.0° F.	95%	*Myotis keenii septentrionalis*	1
Wabasha, Minn.	41.0° F.	100%	*Eptesicus f. fuscus*	10
Dec. 28, 1940	47.0° F.	100%	*Myotis keenii septentrionalis*	1
St. Paul, Minn.	46.5° F.	92%	*Eptesicus f. fuscus*	31
Feb. 15, 1941				

NATURAL LIMESTONE CAVES

Location	Temp.	Rel.Hum.	Species	No.
Spring Valley, Minn.	50.0° F.	99%	*Pipistrellus subflavus obscurus*	4
Oct. 31, 1940	50.0° F.	99%	*Myotis l. lucifugus*	6
	50.0° F.	99%	*Myotis keenii septentrionalis*	1
Mazeppa, Minn.	50.0° F.	100%	*Pipistrellus subflavus obscurus*	24
Jan. 4, 1941				
Marine, Minn.	48.0° F.	98%	*Pipistrellus subflavus obscurus*	4
March 1, 1941				

In each instance the sex was recorded at the time of banding, the temperature of the cave was taken one foot from the resting bats, and a psychrometer was employed to determine the relative humidity of the chambers in the caves.

LARGE BROWN BATS—*Eptesicus fuscus fuscus* (Beauvois)

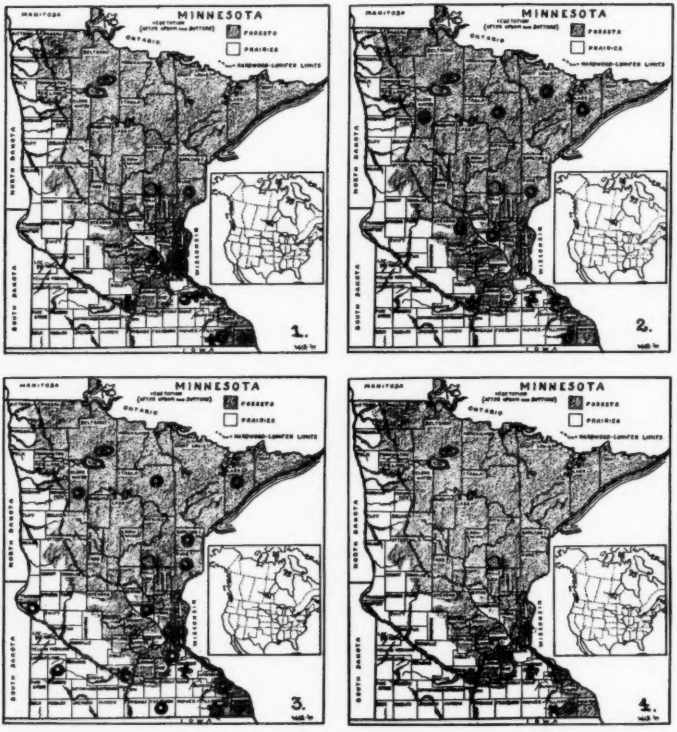
HIBERNATION

Migration to the caves.—It is apparent from literature that but little information is available concerning the life history of this species. Griffin (1940, p. 238) is of the opinion that the large brown bat does not migrate long distances from summer areas to wintering quarters. Although I have no band-

ing evidence to show distances traveled by this species to reach winter caves, I am of the opinion that they traverse many miles in this state during migration. During the summer months this species is one of the less abundant forms, being found rarely in collections and seldom reported; yet in winter I have found then in large concentrations in widely scattered sandstone caves to indicate a gathering from a considerable territory. In the two caves at Red Wing, Minnesota, well over a thousand individuals passed the winter season in 1940-41.

Dates of arrival at caves.—This species is particularly hardy and apparently has the ability to withstand considerable periods of inclement weather and low temperatures. During the fall season the large brown bats remain abroad long after the other cave-inhabiting species have entered the caves for the winter.

On October 24, 1940, the Seven Caves, Nicollet County, Minnesota, were



1. *Eptesicus f. fuscus;* 2. *Myotis keenii septentrionalis* 3. *Myotis l. lucifugus;* 4. *Pipistrellus subflavus obscurus.* ● Summer distribution, ♣ Winter distribution.

examined thoroughly; and at this date only a single *Eptesicus* was discovered, although representatives of the other three species were found in their normal wintering numbers. A search of the brewery cave at Jordan, Scott County, Minnesota, on the same day disclosed no bats of this species.

On November 11, 1940, Frederick Poppe and the writer visited a large sandstone cave at Red Wing, Goodhue County, Minnesota. This cave had been operated commercially in former years for abrasive material but appeared to have been abandoned for some while. Eight large brown bats were discovered after a careful search of each tunnel. The walls of the cave were comparatively smooth and without fissures which might permit concealment of hibernating bats. When we emerged from the cave at 1 p.m., a severe snow storm was in progress; and we left the area immediately.

Thus unusually severe and unseasonal storm of November 11 terminated a mild fall season. The month of October had a mean temperature of 54° F. which was 5.1° F. warmer than normal. The mean temperature of the first ten days of November was 40.5° F. The storm commenced with a drizzling rain which changed to sleet and snow with the falling temperature which reached a minimum of 10° F. during the night. A 42 mile an hour wind accompanying the storm produced a blinding blizzard which caused a considerable mortality among wildlife in general throughout the state.

During the course of this storm, the entrance to one of the two caves at St. Peter, Minnesota, used extensively by hibernating *Eptesicus* was entirely closed by drifting snow. Immediately following the storm, Mr. Meyer, who operates the caves as a tourist attraction, found over a hundred dead bats at the closed entrance. The bats evidently had been overcome by the storm while attempting to gain entrance to the snow-blocked cave. Although several other caves close at hand remained open and accessible, their habit of wintering in this particular cave caused them to continue in search of an entrance until they were exhausted and fell to the snow to die.

The Seven Caves were visited by the writer on December 21, 1940, and Mr. Meyer was questioned at this time regarding the bat mortality. He was thoroughly familiar with the bats which came there each year, and upon questioning him and checking his ability to distinguish the various species, it was decided that the dead bats found were nearly 100% *Eptesicus fuscus*. Cats from a nearby asylum had already carried away the carcasses, and but a single specimen, a large brown bat, was found.

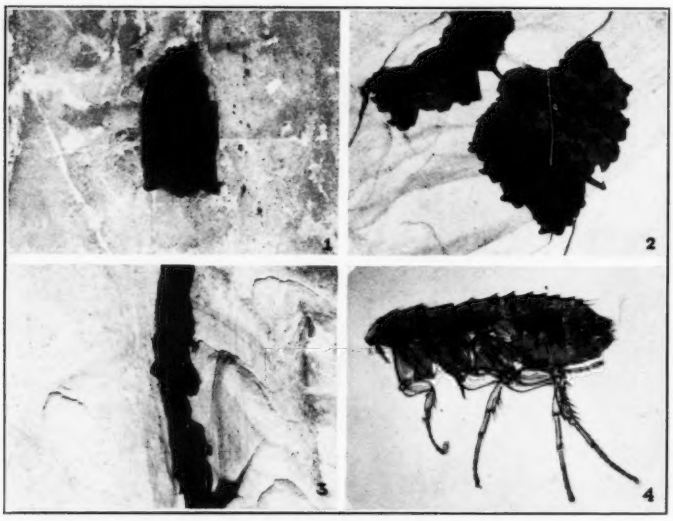
Another of the Seven Caves at St. Peter used extensively as hibernating quarters by this species was examined. Approximately 100 large brown bats were found in this chamber. On March 2, 1939, this cave housed close to 200 bats of this species; and it is entirely possible that many of the individuals customarily hibernating in this cave were too far afield at the onset of the storm to reach this cave and either died in the attempt or chose available temporary quarters elsewhere. A visit to the brewery cave at Jordan, Minnesota, was made the same day. Five large brown bats not present on October 24, 1940 were found.

On January 3, 1941, the sandstone cave at Red Wing, Minnesota, was revisited by Frederick Poppe and the writer. Ten unbanded *Eptesicus* were discovered. These individuals had not been encountered on November 11, 1940, when a careful survey was made of the cave. In all probability these individuals were driven into the cave by the storm of that date, although they may have entered later after having sought temporary shelter.

Russel Berthel reported that during the night of November 11, 1940, at the height of the storm, a large brown bat flew into his room on the second floor of a St. Paul hotel. He released the bat through a window and saw it fly to the protection afforded between two closely adjoining buildings.

An unused mushroom cave at St. Paul, Ramsey County, Minnesota, was examined by Frederick Poppe and the author on November 30, 1940, at which time a total of 12 *Eptesicus* was found and banded. Mr. Poppe revisited the cave on January 8, 1941, and found several unbanded large brown bats in a few minutes' search. In this instance, however, the finding of bats on a subsequent visit does not necessarily indicate arrival after November 30, 1940; for it is entirely possible that some of the bats may have been overlooked on the original visit, as this cave has many inaccessible concealments.

An abandoned cave on Nicollet Island, Minneapolis, Hennepin County, Minnesota, was visited on December 1, 1940. No bats of any species were



Figs. 1-4. 1. *Eptesicus fuscus* female clinging to cave wall as solitary individual. 2. Compact cluster of *Eptesicus fuscus* males on cave wall. 3. *Eptesicus fuscus* will frequently withdraw into fissures. 4. *Myodopsylla insignis* taken from large brown bat.

found in the cave. Five *Eptesicus* from the mushroom cave in St. Paul were released in the Nicollet Island cave at this time. Another visit to the cave was made on January 23, 1941, at which time seven additional large brown bats were found and banded. A visit to the cave on February 23, 1941, revealed two additional unbanded individuals.

These data illustrate well that the large brown bat is hardy and capable of withstanding brief periods of low temperature inasmuch as but few resorted to caves before November 11, 1940. There is definitely a certain degree of influx into the caves in mid-winter as shown in the studies at Nicollet Cave and indicated in other caves. It is probable that these unusually late arrivals were individuals which previously in the season had sought shelter in buildings, later shifting to caves.

Habits associated with hibernation.—During routine banding of this species it became apparent that there existed a tendency upon the part of the males to gather in clusters during the period of inactivity, while the females seemed more given to hanging singly. Commencing on December 12, 1940, a record was kept of the distribution of the sexes in their winter quarters. Table 2 tabulates these data.

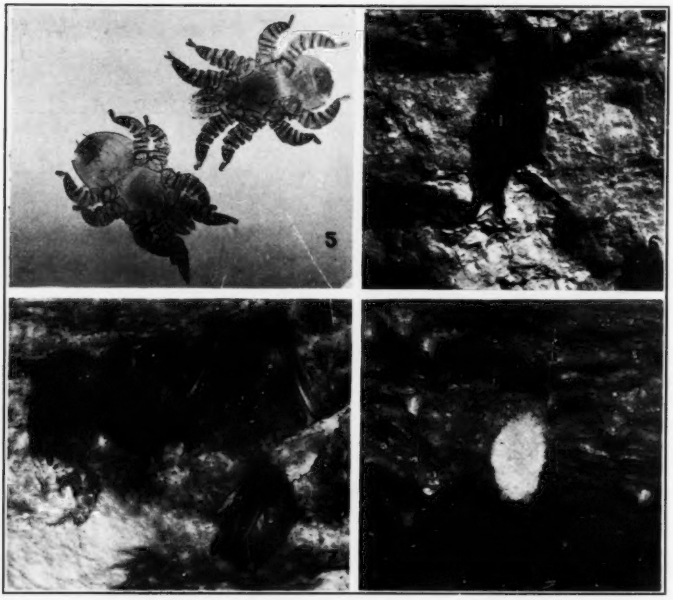
My results are somewhat in contradiction with those of Dr. Mary J.

TABLE 2.—Distribution of *Eptesicus* by sex in wintering caves.

CLUSTERS			SINGLES		
Locality	M.	F.	Locality	M.	F.
Stillwater, Minn. Cave No. 1 Dec. 12, 1940	19	6	Stillwater, Minn. Cave No. 1 Dec. 12, 1940	..	..
Red Wing, Minn. Cave No. 2 Dec. 28, 1940	27	2	Red Wing, Minn. Cave No. 2 Dec. 28, 1940	1	8
Wabasha, Minn. Cave No. 1 Dec. 28, 1940	2	..	Wabasha, Minn. Cave No. 1 Dec. 28, 1940	1	8
Wabasha, Minn. Cave No. 2 Dec. 28, 1940	2	..	Wabasha, Minn. Cave No. 2 Dec. 28, 1940	1	3
Red Wing, Minn. Cave No. 1 Jan. 3, 1941	..	..	Red Wing, Minn. Cave No. 1 Jan. 3, 1941	4	6
Red Wing, Minn. Cave No. 2 Jan. 4, 1941	16	2	Red Wing, Minn. Cave No. 2 Jan. 4, 1941	2	8
	22	2		..	3
	13	..		..	..
Minneapolis. Cave No. 1 Jan. 8, 1941	1	2	Minneapolis Cave No. 1 Jan. 8, 1941	3	1
St. Paul, Minn. Cave No. 1 Nov. 31, 1940	15	3	St. Paul, Minn. Cave No. 1 Nov. 31, 1940	6	11
Total	117	17	Total	18	48

Guthrie who worked with this species in Missouri. She (Guthrie, 1933, pp. 7-8) reports, "Individuals are always isolated when they hang, although when they crawl into crevices, there may be two or three together." She later states, "Among the hibernating forms, males and females are found together." My data show a decided preference of males to gather together in segregated groups, however a few females are usually found intermingled with the males in the clusters.

By many it may be assumed that bats remain in a state of deep torpor in the caves throughout the winter. Such is certainly not true of the species *Eptesicus fuscus*, nor any of the other cave bats, in our state. Whether the winter inactivity of bats should be termed hibernation is questionable, for they are periodically active. The positions of banded individuals in various caves have been charted during this study and subsequent visits have shown clearly that these individuals aroused frequently and shifted their roosting sites. One large brown bat banded on October 24, 1940, in one of the Seven Caves at St. Peter was retaken in another cave about 400 yards distant on December 21,



Figs. 5-8. 5. *Spinturnix americana* is frequently encountered on the wing membranes of the large brown bat. 6. *Myotis keenii septentrionalis* resorts to the caves early in the fall. 7. Dusky Georgian bats in the only cluster found. They are usually solitary in habit while in the caves. 8.*Pipistrellus subflavus obscurus* appears as an albino when covered with droplets of moisture.

1940. Such shifting between caves is perhaps unusual in Minnesota, but movements within the caves throughout the winter are common.

During these periods of activity, the bats apparently seek food and drink. Mosquitoes of several species, cave crickets, spiders, diptera, and lepidoptera, including the beautiful *Scoliopteryx libatrix*, are found inhabiting the caves in winter. These, undoubtedly, furnish winter food. I have never witnessed a bat catch food in the caves, but all individuals removed from the caves to the laboratory dropped well-formed feces. Several times chitin particles have been removed from the mouths of bats during the winter. A banded individual handled several times during the fall of the year was retaken February 2, 1941. In its mouth was a large piece of chitin. This large and conspicuous fragment of chitin could not have been there on December 21, 1940; for on that date this individual had been handled and its teeth examined to determine wear.

Whenever caves are visited, a few bats are found to be active; and on numerous occasions I have seen them lap droplets of moisture from the cave walls.

In this regard, a few observations upon three large brown bats which were kept in captivity during the winter may not be amiss. These were housed in an aquarium covered with screening. The soil on the bottom was frequently moistened, and a composition board cover prevented too rapid evaporation; the temperature remained close to 45° F. The bats remained in resting position and quite motionless for periods of approximately a week each, then would arouse and move about actively. Meal worms and water offered at these times were greedily taken. Shortly after feeding and drinking, they would resume their positions; gradually the respiratory rate would slacken until but one or two barely perceptible inspirations per minute could be noted. In this manner they would remain for another week. Under natural conditions where temperatures are lower, periods of activity might be less frequent. It is possible that the decrease of body water during the inactive period is a factor in arousing them to activity.

Place of hibernation.—Eptesicus shows no inclination to winter in the natural caves of Minnesota. Without exception, all large brown bats have been found hibernating in artificial caves of the sandstone type. These, generally speaking, are much less humid and cooler than natural caves and in most instances are subject to greater degrees of temperature fluctuation.

In the sandstone caves of considerable extent where various latitudes of temperature and humidity are to be found, *Eptesicus* appears to favor the drier and cooler sections, often near the entrance itself. There exists a definite tendency on the part of this species, however, to select sites not directly exposed to drafts.

This species occasionally winters in buildings. I have no records of concentrations of any number during the winter season in buildings, but I have numerous records of single individuals captured in buildings during the winter. Ewanson and Evans (1936, p. 43) write, "In the winter and spring of

1932, Dr. Ralph W. Macy secured a number of bats from a large furniture store in St. Paul. . . . All but one . . . proved to be big brown bats. . . . An additional big brown bat was taken March 1, 1932, at a theatre in Minneapolis, and on December 7, 1934, a student brought one . . . of the same species taken inside the library building of the university."

Two individuals of this species were seen several times during the winter of 1940-1941 in a warehouse building in St. Paul. It appeared at intervals of about a week to fly about in the building. Allen (1940, p. 71) states, "In the latitude of New England this bat frequently winters in city houses or public buildings. . . ."

Temperament during hibernation.—*Eptesicus* is definitely not social with other species of bats during the winter season and is never found massed with individuals of another species. In many instances the hibernation sites chosen by the large brown bat are those with environmental conditions not tolerated by the smaller species. Where *Eptesicus* is found in the same chamber and under similar conditions with *Myotis* and *Pipistrellus,* the large brown bat is invariably segregated from the others. One factor of importance, perhaps, in this consideration is the greater ferocity and strength of *Eptesicus* which may well be feared by the smaller bats.

Even among their own kind, *Eptesicus* sometimes display their irritability. I have seen a disturbing individual in a hibernating mass of large brown bats severely bitten by an aggressive member of the group. This species has strong jaws, and they bite viciously and cling tenaciously. In nearly all instances of my observation, they have administered their bites in the region of the neck and head.

I have found a number of mutilated large brown bats, and these injuries I attributed to such aggressive attacks by their own kind. If these wounds had been suffered from predatory animals, it would be surprising, indeed, that they escaped at all. In a mushroom cave at Wabasha, Minnesota, I found an individual on/in which the left ear was represented by but a mere thread; other individuals showed bloody patches from which the hair had been torn away.

Departure from the caves.—Greater activity among the large brown bats was observed in March, and many individuals which had remained in some of the deeper recesses of the caves were noted near the entrances. It is likely that, incited by brief periods of warm weather, they were making ready to leave the caves.

A female large brown bat which was seen flying about the University of Minnesota campus was captured on March 5, 1941. On March 18, 1941, a dead male was found on the sidewalk of the campus.

In the unpublished field journals of Johan C. Hvoslef translated from Norwegian into English by Mrs. Gertrude Hanson and Mrs. Molly Endresen appears a note under the date of April 4, 1883, for the region of Lanesboro, Fillmore County, Minnesota, stating that on that date a large brown bat had

been captured. The dental formula was given, and there exists no doubt as to the identity.

On April 11, 1941, the cave at Jordan, Minnesota, was visited at which time no large brown bats were found. Presumably all had departed for the summer. On the following evening at Minneapolis four large brown bats were seen in flight at 7 p.m. They remained abroad in the vicinity for some little while, then disappeared one by one; and the last one observed was at 7:40 p.m. These were the only *Eptesicus* seen or reported during the spring season.

SUMMER NOTES

Little is known of this bat in Minnesota during the summer season. No adults with young have been taken, and no summer roost of females has been discovered. Several large brown bats captured in houses in Minneapolis the first part of August were males. Another male specimen was captured July 29, 1941, in St. Paul, and one male was found by Donald Sydow concealed in a cottage awning at Sturgeon Lake, Pine County, Minnesota, on August 11, 1941.

ENEMIES

Vertebrate enemies.—In general, bats suffer few enemies. Perhaps their chief enemies during the period of hibernation are domestic cats, house rats, and vandal boys.

I was considerably astonished in my visits to various caves to find that a great number of them were regularly visited by cats, especially those caves situated near human habitations. Normally, bats hang well out of the reach of prowling cats; but an occasional individual is to be found in a position readily accessible to these enemies. Mr. Meyer of St. Peter related that he had actually seen cats scale walls offering footholds and catch hibernating bats. Following the November 11, 1940, storm, cats visited the Seven Caves at St. Peter, Minnesota, and carried away nearly all the frozen bat carcasses.

E. H. Forbush (1916, p. 68) reports, "Occasionally a low-flying bat is struck down by a cat, or one that has entered a dwelling is caught, but only two observers report to me the destruction of bats by the cat."

Rats, too, undoubtedly claim their toll of hibernating bats; for in several of the caves rat tracks were found. On March 2, 1939, I found remains of an *Eptesicus fuscus* in a rat tunnel in Seven Caves. The remains of another were noted at the entrance of a rat tunnel at one of the Stillwater caves on February 12, 1941.

Vandal boys are destructive when they encounter resting bats in the caves. A horrible account of boys holding burning newspapers close to hibernating masses and burning them to death was told me by Mr. Meyer. The incident took place during the winter of 1940-41 at St. Peter. Many people visiting caves gather specimens to take home as curiosities.

An account of a sparrow hawk *(Falco s. sparverius)* capturing and eating an *Eptesicus fuscus* appeared in the Auk (Stoner, 1939, p. 474). The hawk

was seen to dart at an elm tree trunk and seize a bat of this species, then retire to a perch and consume its prey, dropping a portion of the skull which served to establish the identity of the bat. This incident was noted at 6:30 p.m. at Albany, New York. A. K. Fisher (1893, p. 123) cites a bat in the stomach of a sparrow hawk taken in July, 1870, in Chester County, Pennsylvania; the species was not given.

A great horned owl pellet taken from the entrance of one of the Seven Caves on December 21, 1940, contained a skull of an *Eptesicus fuscus* and a skull of *Blarina brevicauda*. Errington (1940, p. 793) reports remains of a *Vespertilionidae* in the stomach of a great horned owl.

Invertebrate enemies.—Parasites also fall into the category of enemies of bats. Thus far two species of external parasites have been found upon this species during the course of my study. The mite, *Spinturnix americana,* is commonly found in considerable numbers on the upper and lower surfaces of the wing membranes. This genus has been reported from *Eptesicus nilssoni* (Keyserling and Blasius) and *Eptesicus serotinus* (Schreber) of Europe but apparently never for *Eptesicus fuscus* (Beauvois) (Stiles and Nolan, 1931, pp. 723-725). A flea, *Myodopsylla insignis,* was removed from a specimen taken in Red Wing cave November 11, 1940. This genus has never been reported for *Eptesicus* and may be of uncommon occurrence, having been taken but once in this study.

One species of internal parasite has been found in several *Eptesicus* examined and may be of frequent occurrence. It is *Plagiorchis microcanthus* Macy infesting the small intestine (Macy, 1931). A specimen of the large brown bat taken at Jordan, Minnesata, on March 9, 1941, was particularly heavily infested, more than 40 individuals of this parasite having been removed.

All parasites were kindly identified by Mr. A. B. Erickson, University of Minnesota, and are now in the collection of the Department of Entomology and Economic Zoology, University of Minnesota.

Accidents.—Seldom is a bat found which has not suffered some accident to the wing membranes as indicated by the scar tissue nodules. Adept as they are in manuevering about stationary objects, it appears as though they must frequently snag the wings upon twigs and other natural obstacles. Rather severe tears seem to result in little permanent damage, healing over in due course of time and not hindering normal activity in the interim.

MISCELLANEOUS

Voice.—Resting individuals, when first disturbed, utter long and drawn-out raspy and guttural notes. As they become more active, their voices become higher in pitch and clear. When fully awake and alert, squeaky staccato notes are given.

Glandular secretions.—The facial oil glands of this species appear much more highly developed than in other cave bats. When disturbed, the large brown bat emits a pungent odor.

Terrestrial locomotion.—In addition to its skill in flight, the large brown

bat can crawl rapidly and frequently does so. When dormant or semi-dormant individuals are knocked from the cave walls, they are too stupified to fly but are capable of comparatively rapid travel on their limbs. The body is raised on the supports of the hind feet and forearms, and the tail is arched while crawling.

In approaching a roost, the bats fly directly to it, grasping first with the clawed thumbs, quickly invert themselves in to a suspended position, and hang head down. Frequently, upon alighting, instead of inverting themselves, they will crawl into a recess head first. Again, they may first suspend themselves; then using their hind feet alternately, draw their bodies backwards into concealment. On numerous occasions they have been observed to use their mouths in climbing, and clinging in the same manner as a parrot employs its beak.

Color variation.—Nearly all specimens of *Eptesicus* examined have shown slight variation in general fur color, and all gradients from Mummy Brown to dark Van Dyke Brown are displayed. The majority of the Minnesota specimens tend toward the darker shades. Frequently Chestnut blotches of considerable size are found on the belly, and in many specimens slight traces of Chestnut are evident in small restricted belly areas.

DISTRIBUTION

Minnesota distribution.—The entire state is included in the general distribution of this species, however summer records are rarely to be found in collections and little is known of their actual range. The accompanying spot map shows the summer and winter state distribution so far as known to date.

LONG-EARED LITTLE BROWN BAT—*Myotis keenii septentrionalis* (Trouessart)

HIBERNATION

Migration to the caves.—I have no definite information as to the distances traveled to the caves during the fall of the year. Griffin (1940a, p. 235) has shown that this species in the New England states will travel at least as much as 55 miles to winter quarters.

Although this species is rare in museum collections of the state, it is believed to be relatively common throughout Minnesota during the summer season. So little mammal collecting has been done in Minnesota that museum collections are sometimes not a true criterion of relative abundance. Cahn (1921, p. 73) has reported it as common in the state counties during the summer. If this species is as common a summer resident as supposed, the majority of them must certainly migrate to caves in the states to the south of Minnesota; for it is rare in our caves in winter, only a few specimens having been found.

Hitchcock (1940, p. 56) found this species hibernating in a cave at Wiarton, Bruce County, Ontario, on October 28, 1939. In another cave at Wilson's Corner, Quebec, 17 *Myotis keenii septentrionalis* were discovered on November 25, 1939. Gould (1936, pp. 103-104) found 36 individuals of this species in a cave at Cheverie, Hants County, Nova Scotia, on February 11, 1935. It seems odd that wintering specimens should be found in these northern regions

and yet not discovered in larger numbers in Minnesota. Oddly enough, all the specimens found wintering in Nova Scotia and the two taken in Ontario were males.

Dates of arrival at the caves.—This study was commenced too late in the fall to gather data on fall arrival. Bats of this species were found already well established in winter quarters at the Seven Caves, St. Peter, Minnesota, on October 24, 1940. Since that date no influx was noted in any of the caves.

Habits associated with hibernation.—From one of the caves at Red Wing, Minnesota, three individuals were removed from a small drill hole in the ceiling. These three were females. All others have been found hanging singly.

Griffin (1940a, pp. 181-182) states, ". . . (this species is) more often found alone in some small crevice." Gould (1936, p. 103) records, "Most of them (long-eared little brown bats) however were found tightly packed in two drill holes in the roof, which were about five inches deep and one and a half inches in diameter."

Far too few have been found to establish the sex ratio. Mohr (1932, p. 2) found that of 141 specimens collected in Pennsylvania in August and September, 116 or 77% were males. He did not report any segregation of sexes during that season and was not familiar with them in hibernation quarters.

This species has been found in both the natural and artificial sandstone caves of the state, but always they have been found in situations of high temperature and relative humidity. They are periodically active during the winter season. On several occasions a few individuals of this species were seen moving about in the caves while others of the same species were inactive. It has been found associated in clusters with no other species, and I can find no mention in literature that such ever occurs.

ENEMIES

Vertebrate enemies.—This species is probably subject to the same enemies as *Eptesicus*, although its habit of selecting roosts in the innermost chambers of the caves may make it less vulnerable to predation.

Invertebrate enemies.—No parasites have been removed from this species by myself. Stiles (1931, p. 712) reports *Myodopsylla insignis* as an external parasite.

DISTRIBUTION

Minnesota distribution.—The entire state is included in the general range, but only those counties spotted on the accompanying map are validated by specimens or definite observations.

LITTLE BROWN BAT—*Myotis lucifugus lucifugus* (LeConte)

HIBERNATION

Migration to the caves.—This species is the most common bat encountered during the summer months in Minnesota, being stated by Bailey (1929, p. 155) as the ". . . most common of our bats, outnumbering all other species by probably one hundred to one." Yet in winter it is more rare than *Myotis*

keenii septentrionalis in the caves of the state. It has been found in but four caves.

When the St. Peter caves were visited on October 24, 1940, a few bats of this species were found already established for the winter; and no increase in numbers was noted after that date. The exact date at which they enter the caves or usually enter the caves, is not known; but notes gathered by G. Swanson (1941) give some indication of migration dates. He gives the following:

> During the first week of September, 1932, Martin K. Nelson, game warden at Fertile, Minnesota, took me to a farm just a few miles from that town, at which there had been reported a large colony of bats. We were prepared with nets and an apiarist's bellows which we hoped would enable us to catch some of the bats. When we arrived there was not a bat remaining but the farmer assured us that they had left not more than a few days earlier, that is, about the end of August. He reported that there had been a large group of bats, and that they had been spending the daylight hours between the walls of the house. We investigated the spots to which the farmer referred and found large piles of bat dung, so I have no doubt the story was true. The farmer reported that the bats had spent most of the summer in the area, and that their squeaking could be heard every day from within the house. We had no opportunity of seeing even one specimen, but of course they must have been either big brown bats or *Myotis*.

This is an indefinite but interesting record, and in all probability the species was *Myotis lucifugus*, the most common bat of the state and the one usually encountered in such situations.

Bernard Bailey (1929, p. 155) collected specimens of the little brown bat in Sherburne County, Minnesota, on September 16 and 25, 1924. His latest fall record is for one seen October 5, 1921.

An interesting account of migrating *Myotis lucifugus* was reported by Zimmerman (1937, p. 363). At Black River Falls, Wisconsin, on October 29, 1936, hundreds of dead and dying *Myotis lucifugus* were found on the streets of the town. Others were found clinging to the sides of buildings, awnings, and store fronts. He expressed the belief that they had become exhausted during a long flight the night before in their southward migration which had been prompted by a sudden cold wave through the northern portion of the state. It is likely that many of them dashed themselves to death against lighted obstacles in the town; Saunders (1930, p. 225) reports the death of a considerable number of tree bats which struck the lighthouse at Long Point, Lake Erie.

It is evident from the reports of other workers that the annual departure from summer roosts varies considerably. In Iowa, Sherman (1929, p. 321) found over a period of fourteen years that the latest date of departure was October 16 and the earliest date was September 19. The median date on which the roost was deserted was October 3.

In as much as this species is common in summer and rare in winter, it may be assumed, perhaps, that the majority of them migrate to caves situated to the south of Minnesota. Griffin (1940, p. 231), through his banding efforts, has shown that this species will travel as much as 156 miles to its home roost; and it is likely that they are capable of much greater distances of flight.

In the caves of southern Illinois and Missouri this species is found in large

numbers during the winter season. Fifty bats were collected for me at Grafton, Illinois, during the winter of 1940-41. Of this number, forty-five were *Myotis lucifugus* and five *Pipistrellus subflavus*, indicating that the little brown bat was the most common cave inhabitant.

Habits associated with hibernation.—On several occasions little brown bats were found in small crevices, but ordinarily they were to be found hanging singly. Too few were observed to secure data on either sex ratio or sex segregation. A. A. Allen (1920, pp. 56-57) found the sex ratio of young *Myotis lucifugus* to be 48 males to 53 females in New York. Mohr (1932, pp. 2-3), in studying the bats of Pennsylvania, discovered a preponderance of males. Of 406 specimens, 56% were males; in another group of 113, 68% were males. Mohr (1939, p. 44) recorded, "*Myotis l. lucifugus* shows a steady preponderance of males: 64.5 percent in the tunnels and 70 percent in Woodward Cave where six years ago the percentage was 68 percent."

Place of hibernation.—Like *Myotis keenii septentrionalis*, this species has been discovered in both natural and sandstone caves but is always found where high temperatures prevail and where the relative humidity is between 90% and 100%.

Spring dispersal.—The earliest spring record of this species for Minnesota are those recorded by Bailey (1929, p. 155) who observed them in Sherburne County on April 29, 1922, and April 27 and 30, 1923. Hvoslef writes in his journal under the date of May 9, 1882, for the region of Lanesboro, Fillmore County, Minnesota, "There have been bats caught at Iverson's the past few days. Vespertilio subulatus." A diagram of the dentition accompanied the notation to substantiate the species.

Guthrie (1933, p. 17) noted at Rocheport and Hunter's Caves, Booth County, Missouri, that "Indications of movement were noted on February 28 at Rocheport by the occurrence of *M. lucifugus* in a new location nearer the entrance; and on the same day at Hunter's a specimen was taken from the entrance passage. Young ones were now definitely more numerous. Throughout March this species was present, but early in April the numbers were noticeably reduced and the last ones were taken on April 16. . . ."

In these more southern localities, the bats are not as limited by climatic conditions as here in Minnesota. Guthrie (1933, p. 17) writes, "Specimens were quite torpid until mid-January when some activity was observed; numbers increased on February 6 and conspicuously on February 20 after a maximum of 77° and a minimum of 64° F. had been recorded on February 10." The increase in numbers in the caves was credited to northward moving bats. In Minnesota there certainly would be few days before mid-March sufficiently moderate to permit outdoor activity.

Sherman (1929, pp. 320-321) at National, Iowa, found the median date of arrival at the summer roost to be May 13; while the earliest date was May 2, and the latest May 30. It was interesting to note that on three separate years the bats arrived on May 2.

On May 18, 1941, a house at Brownsville, Minnesota, was visited. A great number of *Myotis lucifugus* were found inhabiting the attic. All but one of the captured individuals were females. When the attic was entered, many bats were flying about, while others were found concealed beneath the insulation of the roof. The favorite roosts were indicated by the larger dung piles beneath them.

On June 1, 1941, a single individual was observed by Mr. D. Quimby at the Cloquet Forestry Station, Carlton County, Minnesota, in the northern sector of the state.

A visit was made to Crystal Springs, Winona County, Minnesota, August 16, 1941. In the evening a large number of bats were observed sweeping back and forth above the Whitewater River. With a butterfly net, five individual were captured. Two of these were felled to the river where they swam rapidly by flutter motions of the wings in the water. All were male little brown bats; when banded and released the following morning, each flew directly to the upper branches of nearby trees to take up resting positions.

Young.—Bailey (1929, p. 155) writes that the earliest record of embryos in this species in Sherburne County is May 30, 1925, when three females were collected and two contained embryos. He further notes, "Many specimens have been examined between June 27 and July 10, all of which were at the time nursing, or had recently nursed, young."

One of the two females collected at Brownsville, Minnesota, on May 19, 1941, contained a single embryo in the left horn. This embryo measured 10 mm. from crown to rump in its natural uterine position and weighed 0.32 gram with attached placenta.

Mohr, (1933, p. 52) made several observations upon the young of this species in Pennsylvania. On July 17, two captives gave birth to one young each. At birth, these young weighed 1.45 and 1.55 grams, respectively. During parturition, one of the females rested upon a horizontal screening; the other female hung from a vertical screen head up. The young were partially supported by the pouched interfemoral membrane and partly by the umbilical cord which was not severed but remained attached to the placenta when it was shed. The placenta dried and apparently broke off on the second day.

Mohr (1933, p. 52) reported that at no time did he find females carrying young on leaving the summer roosts. On July 18, he collected 35 male and 33 female bats in the region and supplied the following note:

> The immature bats were easily distinguished from the adults by the darker coloration, a sooty gray above, lacking the yellowish tinge below; by the thicker finger bones and swollen epiphyses; and upon closer examination by the milk dentition and the lighter weight, which on that date ranged from 4.7 to 5.4 grams. In summer the adults range in weight from 6 to 7.5 grams.

Feeding habits.—H. H. Pittman (1924, pp. 231-232) kept several captive *Myotis lucifugus* and made some interesting observations upon their feeding

mannerisms. When a moth had been captured, the bat would settle right-side-up on a near object. The body, wings, and interfemoral membrane were brought into position to form a pouch into which the insect was placed after it had been rubbed down the animal's chest several times. Burying its head in the pouch, the bat would viciously bite the insect a few times and then bring it forth to eat it head first, rejecting the wings which would fall to the ground. This same manner of feeding was observed in the large brown bats which were kept as pets by the author, and it is perhaps the common manner of feeding when large insects are captured.

ENEMIES

Invertebrate enemies.—Several times the mite, *Spinturnix americana,* has been removed from the wing membrane of this bat. The parasite has not been listed for *Myotis lucifugus lucifugus* (Stiles and Nolan, 1931, p. 708). Two fleas, *Myodopsylla insignis,* were taken from a female little brown bat captured at Brownsville, Minnesota, on May 18, 1941.

DISTRIBUTION

Minnesota distribution.—The little brown bat is well distributed over the entire state during the summer months. In winter, as already mentioned, it is rare. The distributional map locates counties of both summer and winter occurrence as known from specimens or authentic observations.

DUSKY GEORGIAN BAT—*Pipistrellus subflavus obscurus* Miller

The Georgian bat is the smallest of the species found in our state, occurring in limited numbers in the caves, both natural and artificial, during the winter season. Until 1934, the presence of this bat in Minnesota was not known. On February 12, 1934, Dr. G. A. Swanson, Dr. Charles Evans, and Dr. W. J. Breckenridge visited one of the Seven Caves at St. Peter, Minnesota, and discovered 15 individuals of this species to establish the first state record. At a later date, Dr. Richard Daggy and Mr. H. T. Peters found this bat in Wabasha County.

D. M. Hatfield (1940) designated our Georgian bat as *Pipistrellus subflavus subflavus.* In examining the specimens in our collection and the live bats in the caves, it became apparent that our forms did not match the descriptions of the subspecies *subflavus.* As a matter of verification, all specimens of this bat were forwarded to Dr. Glover M. Allen who pronounced them to be, without exception, *Pipistrellus subflavus obscurus,* the northern form known commonly as the dusky Georgian bat.

HIBERNATION

Migration to the caves.—This species had already reached the caves of St. Peter, Minnesota, and Jordan, Minnesota, when they were first visited on October 24, 1940; so that no exact dates of arrival are available.

Griffin (1940, p. 237) has banded and traced the migrations of a number of species of bats in the East, and he has recovered *Pipistrellus subflavus* 85

miles from the point where banded, showing that even this diminutive species is capable of migrating considerable distances.

Correlated with the migratory habit is the homing ability of the smaller species of cave bats. They return year after year to the same summer roosts and wintering caves. In 1916, Allen (1921, pp. 53-54) banded four female pipistrelle bats at a summer roost at Ithaca, New York. Three years later three of the four were retaken at the same roost.

The writer captured a Georgian bat on October 24, 1940, at St. Peter, Minnesota. It was banded and released the following day at Minneapolis, Minnesota. When the cave was next visited on February 2, 1941, this individual was recovered in the same cave and very nearly at the same spot from which it was originally taken. To return, this individual had necessarily traveled at least 80 miles.

Place of hibernation.—The pipistrelle bat selects the warm and humid quarters in the natural and artificial caves. In no instance has this species been found where the temperature registered less than 45° F., and usually the temperature of the chambers in which they were found varied between 48° F. and 50° F. The relative humidity in the chambers usually ranged above 95%.

Although this species is reported as social with others of its kind during the summer season, in winter while in the caves it is the most solitary of all the cave bats found in the state. Only once have I found a cluster of Georgian bats, a group of six individuals hanging side by side in the cave at Jordan, Minnesota. In less than a week this group had disbanded and thereafter hung singly.

The Georgian bat, in the winter caves, remains inactive for longer periods of time than the other species; but they periodically arouse and move about. During the time they remain inactive, their bodies become clothed in droplets of condensed moisture; and in torch light they appear almost pure white. In one of the caves at Spring Valley, Fillmore County, Minnesota, I observed a Georgian bat arouse from a state of torpidity. It first showed movement by an occasional shiver; then opened its eyes and peered about with upraised head. The ears, which during the period of resting were somewhat curled or shrunken, were spread open to full size and twitched sensitively; and the wings were exercised. Before taking flight, the bat spent some moments licking the droplets of moisture from its fur, then carefully cleaned itself, scratching its fur and drawing portions of the wing membrane through its mouth.

Spring dispersal.—On April 11, 1941, the cave at Jordan, Minnesota, was visited. At this date the *Eptesicus* had already departed, but all the Georgian bats which had passed the winter there were found in residence. On June 2, 1941, no Georgian bats were to be found in this cave.

At the commencement of this study no summer records existed for this species in the state, and a special effort was made to discover a summer colony. Numerous buildings were examined, but only little brown bats were found

inhabiting them. On August 10, 1941, a visit was made to one of the caves at Spring Valley where three Georgian bats were discovered. One was captured with a butterfly net and proved to be a female. It is not known whether these individuals remained in the cave throughout the summer season and there produced their young or whether they normally return to the caves at this early date. Mr. Pettrey, in charge of these commercial caves, reports that bats are to be found there through the entire summer season.

ENEMIES

No vertebrate predation has been noted. Although a large number were examined for ectoparasites, none was found.

DISTRIBUTION

Minnesota distribution.—Formerly this bat was known from two counties only. It has now been found in six counties in winter and one in summer; likely it is to be found throughout the state in limited numbers during the summer season.

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KEY TO THE BATS OF MINNESOTA

1. Membrane enveloping tail hairy above, naked below ..... 2.
1a. Membrane enveloping tail entirely or mainly naked above and below ..... 4.
2. Total length more than 4¾ inches; wing spread about 16 inches; fur color light grey over yellowish brown .....Hoary Bat *(Lasiurus cinereus)*.

   Description: Size large, total length 5 to 5¾ inches; general fur color Seal Brown and Buff generously overwashed with white, the throat band extending to each ear Naples Yellow, sides of face black and furred; wing membranes thick and leathery, medium to dark brown and heavily furred on anterior half of ventral surface; ears short, oval, furred on inner and outer surfaces, Naples Yellow outline with black, basal lobe large; tragus short, blunt, slightly furred, and incurved.
2a. Total length less than 4¾ inches ..... 3.
3. Wing spread about 13 inches; fur yellowish with overlayer of rich reddish brown modified to varying degrees by ashy tips of hair....Red Bat *(Lasiurus borealis)*.

   Description. Size large, total length 3¾ to 4¼ inches; fur color differs with sex, ♂; general color yellowish with heavy overlay of Kaiser Brown, lower belly much paler, ♀; with Russet wash modified by ashy hair tips; wing membranes medium to dark brown, relatively thick and leathery, and furred heavily on anterior half of ventral surface; ears short, oval, Naples Yellow, basal lobe is prominent; tragus medium length, blunt, basal lobe moderate.

3a. Wing spread about 12 inches; fur dark chocolate brown with frosty tips. ..... Silver-haired Bat *(Lasionycteris noctivagans)*.

Description. Size large, total length 3½ to 4¼ inches; fur color deep Blackish Brown tipped sparingly with silvery white; wing membranes medium to dark brown, thick and leathery; ears short, oval, inner surface naked, outer surface furred on basal half, dark brown, basal lobe prominent; tragus medium length, blunt, basal lobe slightly developed.

4. Total length more than 4⅛ inches; wing spread about 13 inches; fur color wood brown above, paler below..... Large Brown Bat *(Eptesicus fuscus)*.

Description. Size large, total length 4¼ to 4¾ inches; general fur color dark Van Dyke Brown above, paler and more yellowish below; wing membranes dark brown, appear thick, leathery; naked, and outer surface furred on basal half, basal lobe moderate; tragus is straight, blunt, basal lobe large.

4a. Total length less than 4⅛ inches ..... 5.

4. Ears extending noticeably beyond tip of nose when laid forward; tragus long and tapering ..... Long-eared Little Brown Bat *(Myotis keenii septentrionalis)*.

Description. Size medium, total length 3⅛ inches, general fur color Snuff Brown over Blackish Slate above, paler and more yellowish below; wing membranes dark brown, thick and leathery, appear to be naked; ears long and extending 2 to 5 mm. beyond tip of nose when laid forward, light brown, basal lobe moderate; tragus long, narrowed toward backward directed apex, basal lobe moderate.

5a. Ears extending just to tip of nose when laid forward; tragus medium length and nearly equal width throughout ..... 6.

6. Color dark brown; forearm more than 1⅜ inches ..... Little Brown Bat *(Myotis l. lucifugus)*.

Description. Size medium, total length 3 to 3½ inches; fur color is the same as that of *Myotis keenii septentrionalis* in every respect; wing membranes thick and leathery, dark brown, appear naked; ears are medium length reaching just to tip of nose when laid forward, light brown, basal lobe prominent; tragus medium, blunt, directed forward, basal lobe moderate.

6a. Color yellowish brown; forearm less than 1⅜ inches ..... Pipistrelle Bat *(Pipistrellus subflavus)*.

Description. Size small, total length 3 to 3⅜ inches; fur color Blackish Slate at base overlayed by Tilleul-Buff and tipped with light Wood Brown above, somewhat paler below; wing membranes thin, delicate, appear naked, dark brown; ears moderate length, directed forward, light brown, basal lobe small; tragus medium, blunt, basal lobe prominent.

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Book Reviews

PLANT GALLS AND GALL MAKERS. By E. P. Felt, Comstock Publ. Co., Ithaca, N. Y. 1940. viii + 364 pp., 344 figs., 41 plates. $4.00.

Such abnormal plant growths as are called galls properly excite the admiration of the amateur naturalist, and should startle the technically trained plant morphologist and physiologist from his accepted concepts of the capacities of plant tissues and the laws of growth. It is surprising that botanists have not turned more often to galls for an understanding of the fundamental properties and processes of their material. In fact, most of the attention which these structures have received has come from entomologists whose interests have originated through the insects that are responsible for the distortions of the plant tissues. That botanists have not more often been concerned may be due, in part, to the previous lack of a good, comprehensive guide to the existent forms of galls. The present manual and guide to plant galls should, therefore, interest amateurs who have been asking how to identify their collected specimens, and professional botanists and entomologists who are beginning to use galls and gall insects as material for the study of some of the fundamental biologic processes.

There has been, heretofore, no commercially available summary of the galls of the North American continent. The present work originated twenty-seven years ago in an "Illustrated Catalogue of American Insect Galls," which was prepared by Millett Taylor Thompson of Providence, Rhode Island. Thompson left an unfinished manuscript at the time of his death. At the request of the executor of the estate, Dr. Felt, who was then entomologist for the State of New York, edited the Thompson manuscript and published it in 1915. Two years later, Felt published a somewhat extended revision of the Thompson Catalogue (without credit to the original source of the material) as his "Key to American Insect Galls." This was Bulletin No. 200 of the New York State Museum Series. The Bulletin contained most of Thompson's original illustrations with the addition of many other drawings and half-tones, and a short introductory section on biologic aspects of the subject. For twenty-three years this has been the best summary manual of American galls, but it has long been out-of-date and unobtainable on any market. Hence the appropriateness of the publication, through a commercial publisher, of the volume now under review.

This book, like its predecessors, is primarily an illustrated key to American insect galls. Three hundred of its three hundred and thirty-eight pages are occupied with the key. The material is arranged under the names of families and the genera of the plant hosts; and under each host, the galls are grouped as occurring on stem, leaf, flower, fruit, or other part of the plant. The description of each gall is limited to the essential and most distinctive features, often to a single line or two; and there is a great wealth of good drawings and well-printed half-tones that clinch the descriptions of a large proportion of the galls. In all, it is as convenient and workable a key as one could conceive, and a credit to the good sense of the author who intended to produce, not a technical, taxonomic treatise, but a readily usable guide to the published material in this field. After more than twenty-five years' work with one of the gall-making families of insects, the present reviewer still finds the older Felt "Key," and now the new volume, the quickest check of his own memory on American galls.

The volume covers all the insect-produced galls that are known from the North American continent. Thirty-five pages of introduction provide a nice summary of biologic data on the plant growth and their insect producers. There are sections on gall types; general and detailed lists of the insects that produce the galls; a summary of what is known about gall production; a discussion of the life histories of the gall-producing insects, with special emphasis on alternation of generations in the Cynipidae (where Felt records, for the first time, three life histories which have been previously unknown); host relations of the gall-producing insects; a section on the trivial, but

interesting, economic importance of galls; a section on collecting and rearing techniques; and still other items. As far as it goes, this section is well done, and it makes this much of the biology of gall insects available to the general reader, although a thorough summary of the technical literature in this field is still to be done.

While the author had earlier publications on which to base his revision, he deserves great credit for the thoroughness and accuracy with which he has brought the present volume down to date. Our knowledge of American galls has almost doubled since Felt published his "Key" in 1917. In the earlier list, for instance, there were four hundred and forty-five species of gall wasps; there are eight hundred and five in the new publication. Although the volume is based, in large part, upon published descriptions and not upon actual material which the author had in hand, these descriptions are remarkably accurate, and they are capital in pointing out the essential differences between the species involved. There are surprisingly few errors, either in nomenclature, description, or reference, and these are so immaterial that there would be no point in taking space to mention them in a printed review. The author deserves abundant credit for having done well what he intended to do.—ALFRED C. KINSEY, Indiana University.

NESTING BIRDS AND THE VEGETATION SUBSTRATE. By William J. Beecher, Published by the Chicago Ornithological Society, 1942. vii + 69 pp., 1 plate, 10 text figures. $1.00. For sale, Book Shop, Field Museum of Natural History.

This publication is the first of a projected series of studies in the biology of birds, edited and sponsored by the Chicago Ornithological Society. It is an ecological study of the avifauna of Fox Lake, Illinois, and represents continuous intensive observational work on a 482 acre upland-marsh area. Those who have attempted intensive local studies may measure the amount of basic data herein treated when they read that in one season over 1200 nests were located in this area, which was first surveyed from the standpoint of its included types of plant communities. In studying the distribution and density of breeding bird populations, the author rightly points out that in a purely local survey such as this, climatic and physiological factors are largely eliminated. Of the other factors that have been mentioned in literature and which he has had a chance to study in the field, he finds the vegetation substrate to be the most determinate, ".... inasmuch as birds have inherited nest patterns as well as ancestral habitats, which, within limits, predetermine the plant type in which they will nest. It is shown that, though most species have a nesting range through several communities, an abundance peak in one will usually indicate the type best suited to the nest pattern." What Beecher's paper does is to coordinate and to correlate studies of plant ecology and of bird population more completely and thoroughly than has been tried before, and in this it is quite successful. It is a new refinement in explicitness to read, for example, that the sora rail (p. 29) averages a spread of 1.78 acres per nest; that of 54 nests plotted, the botanical distribution is as follows: 1 nest in 10.27 acres of *Typha;* 5 in 5.39 acres of lake *Carex lacustris,* 3 in 39.87 acres of mixed *Carex;* 40 in 36.15 acres of *Calamagrostis;* 2 in 1.38 acres of pond *Carex lacustris;* and 3 in 3.09 acres of pond *Calamagrostis;* or to learn that the pied-billed grebe is largely dependent for nesting substrate upon muskrat activity. Nests of each species are plotted not only by the vegetation substrate, but also by season, and by their vertical distribution.

The "edge effect" is carefully treated, and it is shown that population density increases directly with the increase of edge area per unit of the plant society or with the increase in floristic complexity.

The last topic treated is that of adaptation to changes imposed by man. It is stated that most of the nestings of birds near human habitations are nothing more than range-extensions into newly opened habitat to which they were pre-adapted. Relatively few specialized species have passed with the passing of their optimal habitats. However, those that have specialized most are least likely to be tolerant of environmental change.

There is a useful bibliography, but no index. The lack of an index, however, is not serious in a book no larger than this.—HERBERT FRIEDMANN, U.S. National Museum.

NAME THAT ANIMAL—A Guide to the Identification of the Common Land and Freshwater Animals of the United States with Special Reference to the Area East of the Rockies. By Ernest C. Driver. Privately printed, Northampton, Mass., 1942. 527 pp. $5.00.

In this era of intensive specialization, the generation of general naturalists has disappeared entirely. There are few who from an interest secondary to a program of research and teaching would be willing to attempt the task of organizing the taxonomic material from the many diverse fields of vertebrate and invertebrate taxonomy. Yet this is what Dr. Driver has done in his "Name That Animal." Approaching the matter from the standpoint of stimulating student and amateur appreciation of possibilities of identification of the more common forms, the author has directed every effort toward making even the more technical aspects of determinations seem natural and reasonable.

The treatment of individual groups varies widely in the series of keys. For instance, keys are provided to only the chief orders of Insecta while for the Mollusca, the vertebrates and several other groups the keys aim at recognition of species. The treatment for some groups is intermediate between these two extremes as, for example for the spiders the keys are not available below the family category. In the same key at times some forms are traceable to species while others end with generic ranks. This is not cited as a criticism, for obviously no one volume could carry the entire fauna to species. In most taxonomic courses the instructor adopts a flexible level for class determinations depending upon his personal interests or the availability of keys. In this respect the book under consideration imposes the author's selection of the varied levels for the individual groups rather than leaving full choice to the instructor. Only by some such device of differential treatment could the scope of the text be kept within the limits of a single volume.

In most systematic texts, the keys are arranged in approximately phylogenetic sequence, requiring that the user appreciate the major group of the animal kingdom to which any animal pertains before he can begin the task of operating the keys. In the present book, an attempt has been made to avoid this by grouping together animals of diverse groups that have similar general features. For instance, Coelenterates, Sponges, and Bryozoa are lumped as "Moss-like and Jelly-like Animals."

Apparently in the attempt to present the material at student and amateur level, the drawings throughout are much simplified, are wholly without perspective, and carry no direct evidence as to relative size. These features of the illustrations would not seem out of keeping in mimeographed laboratory directions but in a permanently bound, carefully organized text the blackboard type of simplified drawings with free-hand labels seems rather out of harmony with the standards set by the rest of the book.

Through the introductory materials the author has found occasion to express many patent generalizations. He urges field excursions "more as observation trips than as collecting trips." On conservation, he states: "The hunter and trapper have received more than their share of blame for the decrease in number and species of our wild animals. By far the greatest factor in the decline has been destruction of breeding grounds." And "Another less powerful but never-the-less important factor.... has been the over-protection of a few animals and the ill-advised introduction of foreign forms."

A common misconception is voiced in the Introduction. In crediting Linnaeus with "starting" our present system of nomenclature, he pictures the situation that without Linnaeus there would have been "a different common name in each language for each animal" forgetful of the faact that not only Ray and Tournefort but almost all lesser authorities before the time of Linnaeus utilized Latin names for animals in their works even when writing in their native tongues.

In those groups where nomenclature continues to be troublesome and involved, the author has very wisely cited the authority followed and in many instances he has listed current synonyms that are in common usage as second or third choices in the keys.

The point of view of the experienced teacher attempting to set the material at the level of student capabilities, makes this book a welcome addition to the available texts for laboratory and field courses in systematic zoology.—H. J. VAN CLEAVE, University of Illinois.

GENERAL ENTOMOLOGY. By S. W. Frost. McGraw-Hill Book Company, Inc., New York, 1942. x + 524 pp., 406 figures. $4.00.

That such a volume as this one should finally have appeared is encouraging news to those biologists who have long been fascinated by the activities of insects in their natural environments. This book might well be considered as a compendium of insect biographies. Frost's style of writing is such that the reader's interest never lags.

The book is divided into twenty-three chapters: I. Position of Insects in the Animal World; II. Origin and Distribution of Insects; III. Abundance, Size and Reproductive Capacity; IV. Beneficial and Injurious Insects; V. Orders of Insects; VI. Metamorphosis; VII. Immature Insects; VIII. Morphology; IX. Color; X. Sonification; XI. Behavior; XII. Associations, Including Social Insects; XIII. Solitary Insects; XIV. Scavengers, Predators and Parasites; XV. Plants and Insects; XVI. Leaf-minnig Insects; XVII. Leaf-rolling Insects; XVIII. Gall Insects; XIX. Boring Insects; XX. Sutberranean Insects; XXI. Aquatic Insects; XXII. Case-making Insects; XXIII. Cessation of Activity.

Frost is a specialist on leaf-mining insects, but he did not permit this phase of the work to get out of bounds. His chapter on leaf-miners fits well into the scheme of chapters which follow. In fact, the volume, in general, is rather well organized. That the chapter on morphology succeeds rather than precedes the chapters on insects orders, metamorphosis and immature insects could well be considered faulty organization; and yet there is nothing to prevent the student's beginning with Chapter VIII.

The reviewer had long awaited a textbook of general entomology, and as a teacher he had felt that no adequate textbook of elementary entomology had been published. So when Frost's work appeared he was most anxious to try the book "under fire." Such an opportunity was presented to him, and the results of the book's use were, in general, very satisfactory. Not that the volume is without errors. One has the impression that the author had a press deadline to meet. Errors appear in the otherwise excellent and exceedingly useful bibliographies which follow the chapters. The keys to immature forms of insect orders and of families of Lepidoptera and Coleoptera, which are part of an interesting and informative appendix, require much reworking. One is unable to key those many dipterous larvae which possess well-sclerotized head capsules. Many larvae of Lepidoptera and Coleoptera are very difficult or even impossible to key accurately. Some common families (such as Cicindelidae) of Coleoptera have been omitted from the key, while families of less frequently observed larvae (such as Silphidae) are included. The reviewer is well aware of the difficulties involved in formulating keys to immature insects; therefore, he is especially anxious to see relatively simple accurate keys in textbooks.

The most serious criticism which can be made must be directed at the openly teleological vein of the book. If one believes that the groups of insects with well developed social behavior possess an intelligence, he may be soundly scientific regardless of how he may explain the behavior of those insects. But when purposive behavior is written into all the activities of all insects the teleologist cannot hope to escape an argument. "The purpose of," "in order to," and other such phrases, appear frequently throughout the book; and yet the author closes his chapter on insect behavior with the following comment: "Even though we agree that insects seem to memorize certain acts or images, we must admit that they cannot recall them at will. They are therefore incapable of reasoning or understanding."

As the first genuine elementary textbook of general entomology, Frost's volume is outstanding. The author has accomplished an exceptional piece of work, and his ability to condense and organize a mass of interesting material in an instructive and elemental manner is most commendable. The book is highly recommended to college and university students and to high school biology teachers who wish to acquire their first taste of entomology. The figures (many of them are photographs) are plentiful and excellent, and the index is quite complete. The perennial binding, fine quality paper and clear type are much to the owner's advantage.—A. C. COLE, JR., University of Tennessee.

FERNS AND FERN ALLIES OF LOUISIANA. By Clair A. Brown and Donovan S. Correll, Louisiana State University Press, Baton Rouge, Louisiana, 1942. 182 pp., illust. $3.00.

This volume on ferns and fern allies is a unique contribution to the botany of Louisiana. Although various groups of the flowering plants of the state have attracted some attention, none have received the exhaustive treatment given here to the pteridophytes. The purpose of this book, as stated by the authors, is "to aid those interested in Louisiana ferns to identify the various species and to give as much information about them as possible."

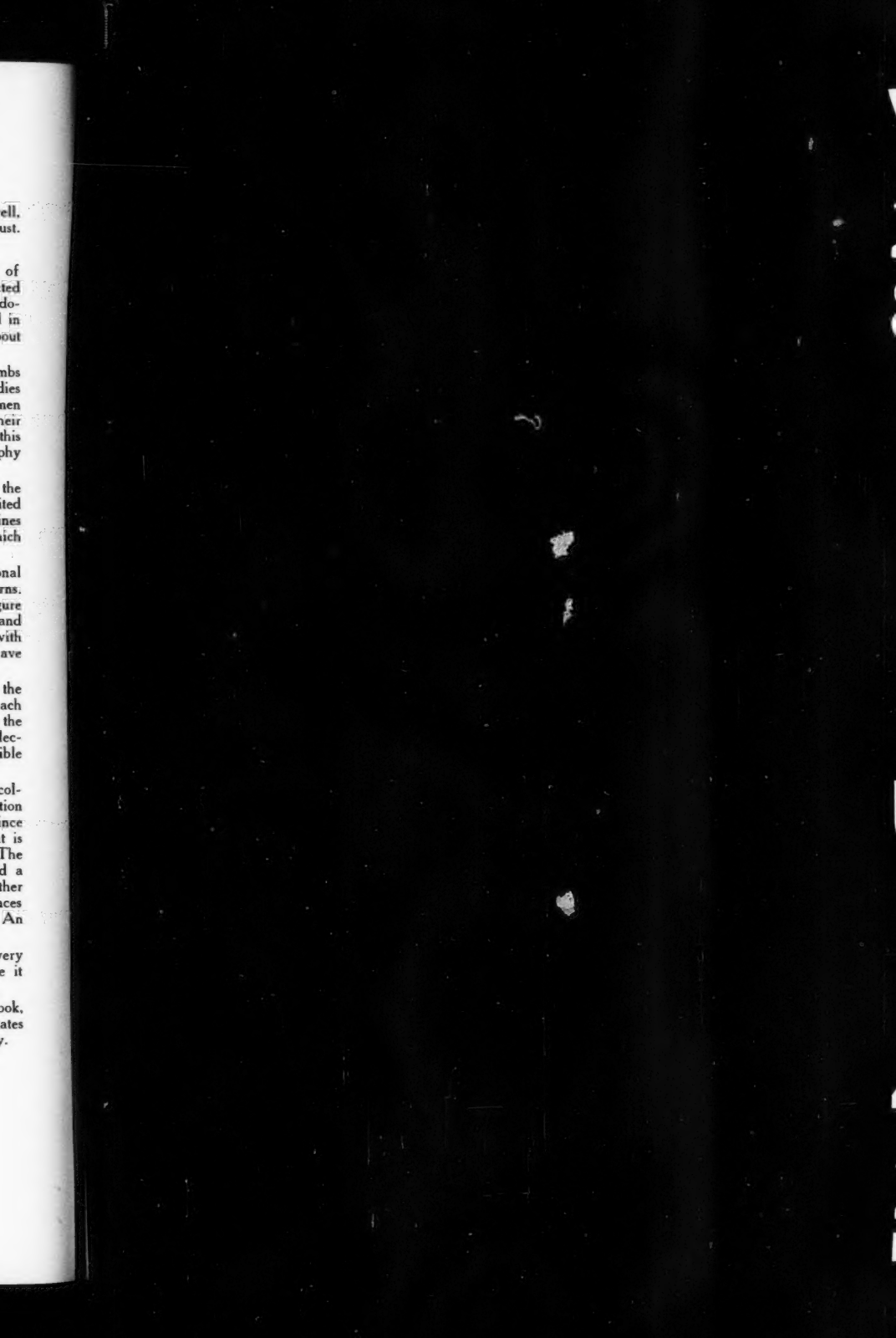
That the above declaration is an understatement will be evident as the reader thumbs through the excellent introduction. For example, in the section headed "Previous Studies on Louisiana Ferns," he will find the best work which has been published on the men who have collected plants in Louisiana. Additional notes on these collectors and their collections are sprinkled liberally throughout the rest of the text. Furthermore, this volume contains the most important exposition to date on the relation of physiography and geology to plant distribution in Louisiana.

The authors discuss the manner in which Pleistocene glaciation has affected the present-day fern population of the state. They point out species that seem to be limited to one or more of the interglacial terraces and list others found in deep, cool ravines which have "stayed on in suitable habitats" as relicts of a former vegetation which migrated northward with the melting of the last ice sheet.

As the book is designed for use by the amateur naturalist as well as the professional botanist, an attempt is made to acquaint the former with the essential structure of ferns. Although the discussion on morphology is reasonably complete, it is felt that the figure delineating the various peculiarities of structure found in ferns is unduly crowded and inadequate for the novice. This is partly compensated for by an excellent glossary with references to photographs, scattered throughout the book. However, one could have wished for more of the beautiful inserts showing enlarged fruiting portions.

In their presentation of the Louisiana ferns the authors include a key to the families, a description of the families (total 13) followed by keys to the genera in each family. Descriptions are given of the genus, the species and, where present, of the varieties. The notes on individual species are followed by lists of the Louisiana Collections. Interesting facts as to the origin of each plant name are given whenever possible as well as facts regarding the habitat and distribution of each species.

"The specimens are cited as follows: Parish, location with the parish, year of collection, collector, collector's number, and the herbaria where the particular collection may be found." The authors include citations from thirteen different herbaria. Since "no ferns have been included on the basis of previously published reports" alone, it is possible to check all reported species by reference to herbarium specimens. The authors list sixty-six species, varieties, forms and hybrids. In the glossary they add a few species "which have been found in adjacent states and which may with further collecting be found growing in Louisiana." The bibliography of eighty-two references should prove of considerable value to botanists throughout the Southeastern States. An excellent index brings this small volume to a close.

The merits of this book are such that it should find a place on the shelves of every lover of ferns in this state. I should also claim more than state-wide interest since it includes most of the ferns of East Texas, Arkansas, Mississippi, and Alabama.

Since many relatively new and thought-provoking ideas are presented in this book, it is felt that all amateur and professional botanists in Louisiana and adjacent states should profit by the use of this book.—WILLIAM T. PENFOUND, Tulane University.